# HYDRAULIC DISTURBANCE AS A DETERMINANT OF PERIPHYTON DEVELOPMENT IN STREAM ECOSYSTEMS

A thesis presented for the degree of

**Doctor of Philosophy**

Department of Zoology
University of Canterbury, Christchurch,
New Zealand

by

**Barry J. F. Biggs**

**January 1996**

**Dedication**

## To Wendy and Hamish,

for their unfailing support through the years.

# TABLE OF CONTENTS

## GENERAL PREFACE

Field ecology has generally focussed on the quantification of patterns in the distribution of biota and attempted to explain these by comparison with variations in habitat conditions. This approach generates hypotheses about causal mechanisms which can be tested experimentally. Such approaches have been used in stream ecology and these have highlighted the role that natural physical disturbance may have in determining patterns in the distribution and abundance of taxa among streams of different regions.

In recent years, there has been a great increase in effort to understand factors controlling the distribution and abundance of stream periphyton communities. Awareness has grown of the importance of these communities as food for invertebrates (and thus as a fundamental energy base for streams), as excellent indicators of environmental change, and on a less positive note as causes of degradation in water quality and aesthetic values. The importance of flood disturbance as a determinant of periphyton development has been clearly shown in many early studies (see Chapter 1). In-fact from first principles alone it can easily be argued that streams with a high frequency of flood disturbances are unlikely to suffer from enrichment and nor are their communities going to be subject to heavy invertebrate grazing control. Conversely, nutrients and grazers are likely to become increasingly important with time since the last disturbance event and thus require long interdisturbance stability to be a significant determinant of community development. It is highly possible that the disturbance regime is the most important determinant of community development in streams of the temperate region. However, much of the research undertaken between 1989 and 1995 has focussed on grazing and nutrient enrichment processes in hydrologically stable, continental, streams. Only a limited number of studies have extended our understandings of the importance of disturbance as a major factor controlling periphyton community structure, biomass and production in streams.

The goal of the following set of studies was therefore to more clearly define the role of hydraulic disturbance in determining the development of periphyton in streams, and to provide a physical basis upon which disturbance intensity and frequency could be defined. Using this approach I hoped to obtain a much clearer understanding, and ultimately to produce a predictive model, to explain why periphyton communities of streams in one region can be so different from those in another. Following a general review of patterns in periphyton development in natural streams, and an elucidation of the potential importance of hydraulic disturbance in determining these patterns

(Chapter 1), I describe a broadscale study of 16 New Zealand streams which investigates the importance of differing disturbance frequencies in controlling average periphyton biomass over a whole year. The contribution, and interactive effects, of nutrient resource supply in determining this pattern are also investigated (Chapter 2).

In the third chapter, I describe an experiment designed to determine what shear stresses are required during flood events to dislodge different types of periphyton communities, and thus also determine removal kinetics and resistance properties. In Chapters 4 and 5, I investigate community redevelopment as functions of spatial variation in hydraulic conditions in a stream. Hypotheses are tested regarding differential colonisation, growth and sloughing dynamics in relation to time since a disturbance, and the interaction of these dynamics with hydraulic conditions on the falling stage of the hydrograph.

In Chapter 6, I attempt to establish a conceptual basis for understanding the effects of disturbance on periphyton community development and to explain how this interacts with limiting resource supply and invertebrate grazers as major components of the habitat matrix of stream periphyton. This conceptual model is tested using both field (Chapter 7) and experimental (Chapter 8) studies. The field study involved monitoring periphyton development at multiple locations which varied in disturbance and nutrient supply regimes within a single catchment. Average development over a two year period was then compared with predictions made under the disturbance - resource supply - grazer conceptual model. In the experiment, periphyton communities were grown under varying degrees of light and nutrient resource stress, and the effects of a single, simulated disturbance measured in terms of community resistance, resilience and mean biomass. These results are compared with the predictions of the conceptual model.

The chapters in this thesis are presented in the form of manuscripts that have been, or will be, submitted to various scientific journals. Inevitably, this has resulted in some repetition of material (particularly review material in the Introductions), and some differences in format including the citation of references. Nevertheless, I have attempted to standardise the layout of chapters as much as possible, and have provided some continuity to the thesis by including linking sections in the form of short prefaces before each chapter.

## GENERAL ACKNOWLEDGMENTS

A vast amount of data has been collected and summarised in the following thesis. This has only been possible because I am supported by a very capable group of field and laboratory technicians. It has not been possible for me to be part of every sampling trip or even process a fraction of the samples collected myself. I have, however, carefully trained my technical staff in all periphyton sampling and analytical methodologies. Through regular montoring of activities and QA checks, I am very confident in the quality of the numbers that have been produced for my studies. You are referred to individual chapters for specific technical acknowledgments.

The preparation of this thesis has been made possible by the sponsorship of the staff and management of the National Institute of Water and Atmospheric Research (in particular Sally Davis and Clive Howard-Williams). I greatly appreciate their support.

Two people require individual recognition at this point. Firstly, Professor Mike Winterbourn has been an enthusiastic perveyour of the science of stream ecology in New Zealand over the last 20 years. He has been at the forefront of our efforts to elucidate the biological processes in New Zealand streams and then enunciate these to our fraternity worldwide. His findings, and teachings, have now permeated through most textbooks and have put our great outdoor stream laboratory on the international map. I thank him for this. I also thank him for the great opportunity of finally enrolling under him as a Ph. D. canditate. While much of the research for this degree has been carried out off-campus, it hasn't been done without his considerable influence, particularly through the very constructive reviewing of many of my past manuscripts and all of the following chapters. Thanks for your great contribution Mike.

Finally, I wish to thank Wendy: friend and mentor. It wouldn't have been possible without you.

## SPECIFIC CHAPTER ACKNOWLEDGMENTS

**Chapter 1**

I am grateful to Jan Stevenson and Rex Lowe for their constructive reviews.

**Chapter 2**

I thank the NIWA Environmental Data collection teams for carrying out the sampling and flow monitoring, Greg Tod and Jenny Templeton for nutrient and biomass analyses, Philippe Gerbeaux for assistance with taxonomic analyses, and Kathy Walter and Richard Jordan for assistance with datalogging. I thank Chris Peterson, Alastair Suren, and Jan Stevenson for review comments on earlier versions of this chapter. This study was funded in part by the Department of Conservation (contract S3040/327) and the New Zealand Foundation for Research, Science and Technology under the NIWA 'Streamflow Variability' programme (Contract CO1319). I am very grateful for their support.

**Chapter 3**

This research was carried out under the NIWA "River Ecosystems" and "Streamflow Variability" programmes funded by FRST (Contracts CO1210 and CO1319). I am grateful for the assistance of Alan Stokes in building the flow tank and with design modifications. I also appreciate the technical assistance of Henrik Thomsen, Nelson Boustead and Marianne Biscard-Thomsen.

**Chapter 4**

I thank Geoff Price for technical assistance and Dr Siri Stokseth for making available the data from Norway. The data analysis and writing of this chapter was carried out with support from FRST under the "Streamflow Variability" programme (Contract CO1319).

**Chapter 5**

I thank Chris Hickey for assistance with designing the sampling programme and field work. I am also grateful to Philippe Gerbeaux and Cathy Holmes for assistance with laboratory analyses; Rex Lowe, R. Jan Stevenson, and Ian Hawes for constructively reviewing the chapter.

**Chapter 6**

I thank Jan Stevenson, Rex Lowe, Nancy Tuchman and Bob Pillsbury for input to the allocation of taxa to the various guilds and discussions of the disturbance - resource supply grazer concept. I am also grateful Rex Lowe for his review comments on the chapter. The majority of this work was carried out under the project

"Dynamics of Small Catchments" (Contract CO 1302) from the New Zealand Foundation for Research Science and Technology. I am grateful for their support.

**Chapter 7**

I greatly appreciate the assistance of Peter Stephens and colleagues, Otago Regional Council, who carried out the monthly periphyton sampling, hydraulic measurements and water nutrient analyses. I also thank Cathy Kilroy and Faye Richards for carrying out nutrient and periphyton analyses, and Richard Pooley, Brian Smith and Derek Kater for assistance in the field. This research was partly funded by the Foundation for Research, Science and Technology under the "River Ecosystems" programme (Contract CO1210 of Output 32) and the BGSU Faculty Research Committee. I am grateful to Dr Jim Teeri and the University of Michigan Biological Station for support during the preparation of this chapter.

**Chapter 8**

The experimental design benefitted from discussions with Drs Nancy Tuchman, Jan Stevenson and Rex Lowe for which I am grateful. I also appreciate the technical assistance of Alyssa Tomoff, Ruthann Schulte, Andrew Gagne, Jennifer Greenwood and Mike Grant. The funding and organizational assistance of Nancy Tuchman, Rex Lowe, Dr James A. Teeri and the National Science Foundation in developing the experimental stream facilities at the University of Michigan Biological Station and for technical support was fundamental to the successful completion of the experiment. Financial support for me came from the University of Michigan Biological Station, the New Zealand Foundation for Research Science and Technology (Long-term Effects of Streamflow Variability Programme, Contract CO1416), and the Joint US-NZ Co-operative Science Agreement administered by NSF and the New Zealand Foundation for Research, Science and Technology. I thank Nancy Tuchman, Rex Lowe, Jan Stevenson and Alex Ross for review comments.

Finally, I wish to thank my external examiners Prof. Colin Townsend and Dr Colbert Cushing for their detailed analysis of this thesis. They provided many useful comments and queries which have helped clarify the text. I greatly appreciate their input and positive evaluation.

# Chapter 1

## A Synthesis of Patterns in Stream Periphyton Development

## I. Introduction

Periphyton are the most successful primary producers to exploit streams as habitat. They are widely considered to be the main source of energy for higher trophic levels in many, if not most, unshaded temperate region streams (e.g., Minshall 1978). Periphyton also sequester inorganic nutrients and labile organics thereby helping to purify stream waters (e.g., McColl 1974, Vymazal 1988). However, in stable-flowing, enriched streams they can proliferate causing water management problems (e.g., Trotter and Hendricks 1979, Wharfe et al. 1984, Biggs 1985a). Because of their rapid response to environmental change they are also useful as indicators of stream water quality (Whitton 1979, Biggs 1985b, Biggs 1989, Biggs 1990a, McCormick and Cairns 1994).

Four reviews of the ecology of stream periphyton have been published (Blum 1956, Hynes 1970, Whitton 1975, Lock 1981). In these, aspects of the distribution of common taxa and biomass are discussed in the context of environmental regulators such as current, substratum type, temperature and light. However, since these reviews, much has been learned about the effects of other factors including nutrients, disturbance and invertebrate grazing. A summary of these factors classified according to whether they contribute to growth or loss processes is given in Fig. 1.1 (the role of these factors in determining pattern will be elaborated on later in the chapter). The opportunities presented by new analytical technologies such as computer-based GIS and multivariate statistical systems have also enabled the definition of broader scale relationships between periphyton communities and their terrestrial settings of geology, landuse, and climate (e.g., Biggs 1990b, Leland 1995).

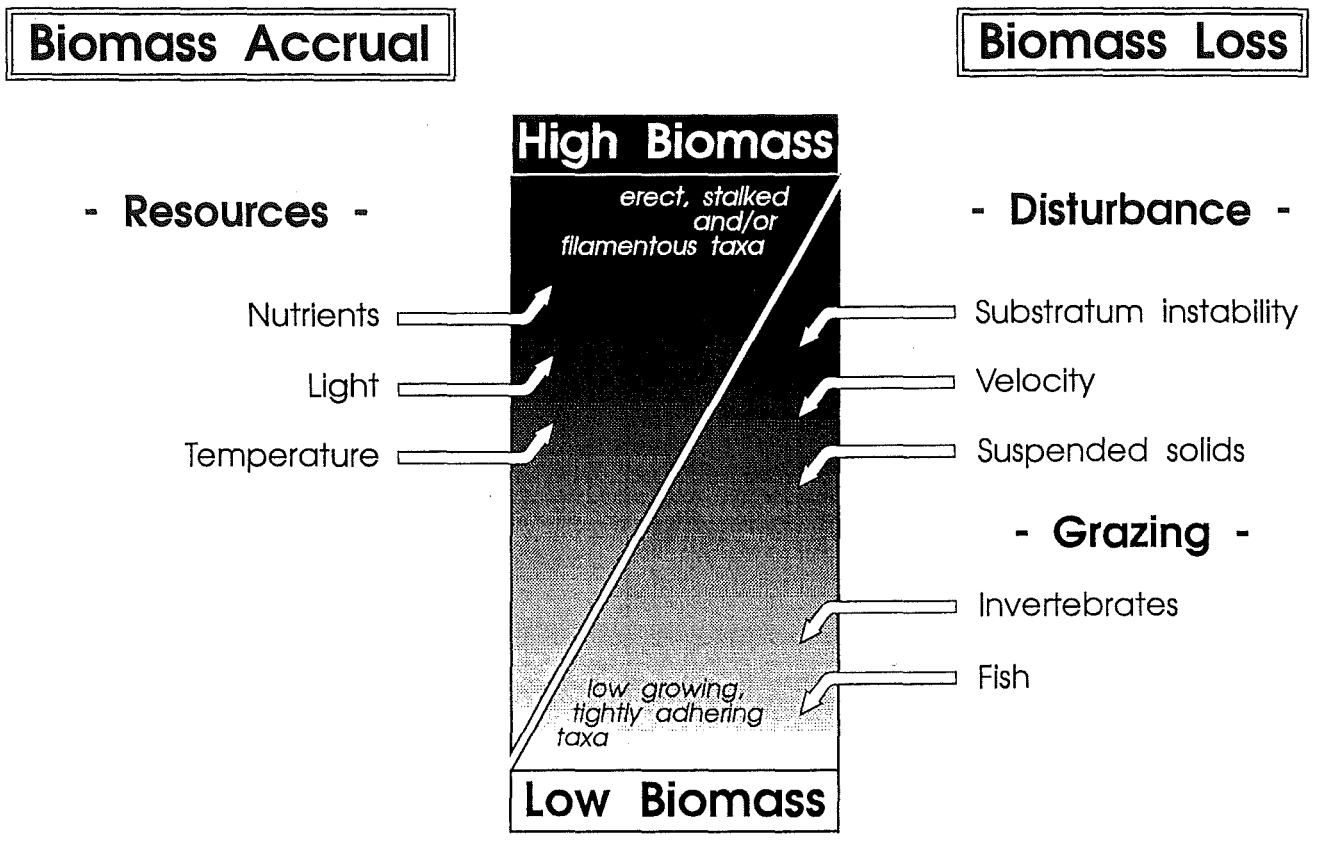


Figure 1.1: Summary of the main factors regulating the accumulation of periphyton biomass in streams. The relative balance of 'biomass accrual' and 'biomass loss' processes is depicted by the width of the triangles which make-up the central rectangle. The physiognomy of the community likely to dominate each end of the gradient is also shown.

The following chapter on patterns in biomass and taxonomic structure of stream periphyton is based very much on recent understandings of the ecology of this community. It is not intended to be a comprehensive guide to the literature, but an attempt to identify some general patterns in natural streams. In so doing, I only draw from the extensive literature of experimental studies where it is necessary to illustrate a particular process. Temporal and spatial dimensions are addressed separately, although the two are partly interlinked in determining pattern. The following synthesis also considers a range of scales, from patterns occurring on individual substrata over periods of weeks, to patterns that persist over periods of years, and which can be evident across continents. This synthesis should assist with understanding local, regional and broadscale community structure and dynamics. It will also provide a framework for the placement of later Chapters in the thesis.

## II. Temporal Patterns in Stream Periphyton

*Short-term patterns*

A clear, and generally universal, pattern of short term periphyton biomass accrual is evident in streams (Fig. 1.2). It has been shown for introduced artificial substrata (Cattaneo et al. 1975, Biggs 1988a), at the commencement of experiments in artificial channels (e.g., Bothwell 1989, Reiter 1989, Peterson and Stevenson 1990, Poff et al. 1990, Mulholland et al. 1991) and in natural streams following floods (e.g., Biggs 1988b, Scrimgeour et al. 1988). This pattern in biomass reflects a shift in importance among the primary accrual processes. Accrual through immigration/colonization and growth dominates early in the sequence (termed the 'accrual phase' on Fig. 1.2) (e.g., Bothwell et al. 1987), but then there is a shift to dominance of loss processes through death, emigration, sloughing and grazing later in the sequence (termed the 'loss phase', Fig. 1.2) (Stevenson 1986).

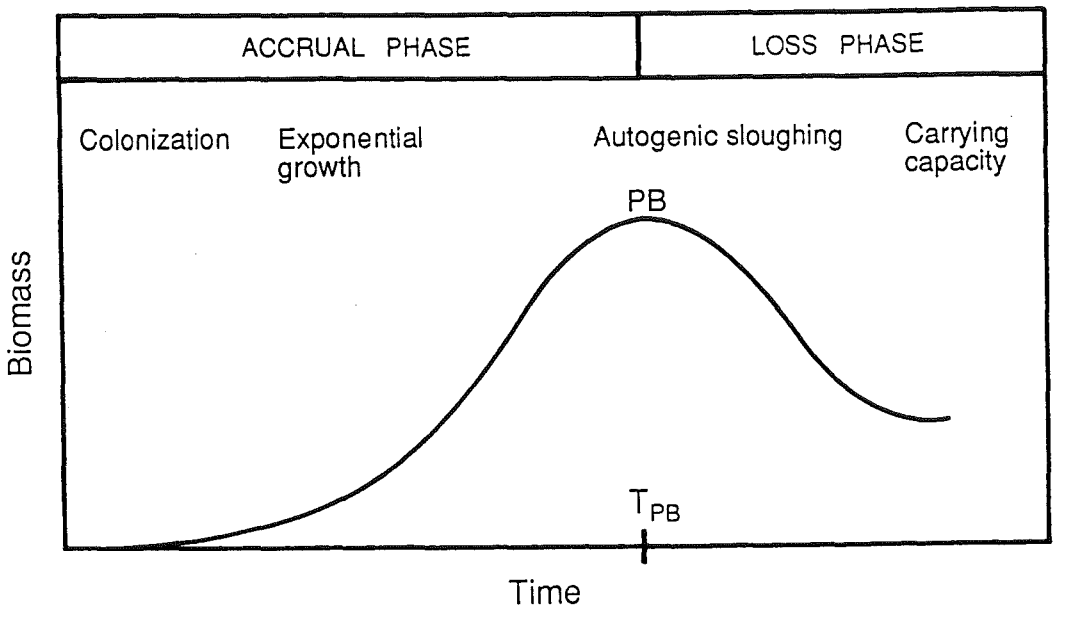


Figure 1.2: An idealised periphyton accrual curve with different phases shown. PB (Peak Biomass) is the maximum accrual cycle biomass and $T_{PB}$ is the time to PB from commencement of colonization.

Immigration/colonization is a linear process dominated by passive settlement of cells (Bothwell et al. 1987, Stevenson and Peterson 1991). The settlement rate is governed by the size and type of the propagule pool (related to the abundance of cells in upstream refugia formed by bedrock, bryophytes, and seeps), immigration and dispersal properties (such as cell size/morphology), substratum texture, water velocity, and light intensity (Jones 1978, Kaufman 1979, Osborne 1983, Stevenson 1983, Bothwell et al. 1989, Peterson and Stevenson 1990, Stevenson and Peterson 1989, 1991). A succession often occurs, beginning with the development of an organic matrix and bacterial flora followed by a transition from small adnate diatoms (Bacillariophyceae) to apically attached colonial diatoms, and finally to filamentous green periphyton (Chlorophyceae) (e.g., Hudon and Bourget 1981, Korte and Blinn 1983, Peterson and Stevenson 1990). After settlement, the colonizing cells undergo exponential growth at a rate dictated by the availability of resources and the cells'

modes of reproduction (Fig. 1.1, 1.2) (Stevenson 1986, Bothwell 1989). In unshaded streams, the most important of these resources are nutrients (e.g. Lowe et al. 1986), but in heavily shaded streams, low light levels may be the primarily limiter of growth (Fig. 1.1) (Hill and Knight 1988, Boston and Hill 1991). Exponential cell division at this time results in exponential development of mat biomass early in the accrual cycle (Fig. 1.2). Later, kinetics become progressively linear as the newly synthesized biomass becomes small compared with that already accrued.

The proportion of new cells that can accumulate appears to be determined by the degree of non-catastrophic losses through current-induced drag (e.g. Biggs and Close 1989, Peterson and Stevenson 1992), emigration (Stevenson 1986, Stevenson and Peterson 1989, 1991) and grazing (e.g., Winterbourn and Fegley 1989, Winterbourn 1990, Rosemond et al. 1993) (Fig. 1.1). The time taken to reach peak biomass ($T_{PB}$, Fig. 1.2) varies. Following low to moderate intensity floods, colonization can be rapid (Stevenson 1990), probably because of the availability of a high abundance of propagules in refugia. If this is also followed by rapid growth, peak biomass (PB) may be reached within two weeks (e.g., Stevenson 1990). However, following more complete depopulation by severe floods colonization may take many weeks, and if growth rates are low, time to peak biomass ($T_{PB}$) can be > 70 days (e.g., Fisher et al. 1982, Biggs 1988b). Intuitively, one would expect $T_{PB}$ to be shorter in enriched than unenriched streams because specific growth rates should be higher (e.g., Horner et al. 1983, Bothwell 1989), however, this is not necessarily so (e.g., Biggs 1988a, Lohman et al. 1992). This apparent paradox appears to be due to the earlier onset of nutrient limitation at the base of an accumulating periphyton mat in nutrient poor waters, resulting in mat degradation and sloughing early in the accrual cycle.

PB values (Fig. 1.2) vary asymptotically as a function of nutrient loading during the growing period (Horner et al. 1983, Bothwell 1989, Kjeldsen 1994). Higher nutrient levels are likely to maintain higher diffusion gradients within periphyton

mats allowing them to develop into thicker structures (e.g., Horner et al. 1983). However, some variation in PB values can be expected for given nutrient loadings depending on other constraints such as water velocity (e.g., Horner et al. 1983, 1990, Biggs and Gerbeaux 1993). Maximum PB values (termed $PB_{max}$, Bothwell 1989) at high nutrient loadings vary for different communities and can range from 300 - 400 mg $m^{-2}$ chlorophyll *a* for diatoms and cyanobacteria (Cyanophyceae) (Bothwell 1989, Horner et al. 1990) to > 1200 mg $m^{-2}$ chlorophyll *a* for filamentous green and chrysophyte periphyton (Chrysophyceae) (Kjeldsen 1994 and pers. com.).

Biomass accrual slows when losses approach the rate of accrual (Fig. 1.1, 1.2). Although little studied, these losses probably occur through a combination of death due to age, parasitism, disease and removal by grazing. Very rapid losses often occur as autogenic sloughing (e.g., Biggs and Close 1989). This appears to be a function of resource stress of the underlying layers (e.g., Dodds 1989, 1991). Eventually, loss processes dominate (i.e., the community enters the loss phase, Fig. 1.2), and carrying capacity is reached when rates of accrual and loss are more or less in balance. The biomass at which this occurs varies greatly. For example, in some situations carrying capacity approximately equals PB (e.g., Oemke and Burton 1986), but often it is less (e.g., where communities are dominated by diatoms) (Biggs and Close 1989). Factors probably affecting this balance include rates of metabolite mass transfer to the base of the mats, grazing, hydro-dynamic shear stress and mat tensile strength.

During the accrual cycle there is also a continual loss of cells through emigration, a process that often peaks during day time (Stevenson and Peterson 1991, Barnese and Lowe 1992). The concentration of drifting emigrants is generally related to abundances of periphyton on the bed (at least for diatoms) and although drift composition reflects communities in general terms, there can be interspecific differences in drift activity (Stevenson and Peterson 1991).

It should be stressed that these short-term biomass dynamics will probably be masked by variability if the spatial resolution of sampling is either too fine or too coarse. For example, quantifying dynamics at a small (say, cobble) scale will reveal much greater variability in biomass than the idealized accrual cycle shown in Fig. 1.2 would suggest. Patchy distribution occurs over individual substrata through variations in growth and loss due to spatial variations in hydrodynamic conditions (Stevenson 1983), and densities of grazers (Downes et al. 1993). Conversely, periphyton sampled at larger spatial scales may incorporate several different habitat units (e.g., riffles, runs and pools), within which growth rates may vary so that accrual cycles may not be synchronized. Thus, to identify accrual dynamics (such as that depicted in Fig. 1.2), may require many (e.g., > 10) samples which are stratified according to habitat units.

*Long-term patterns*

Three main long-term temporal patterns in periphyton biomass can be distinguished among streams: 1- relatively constant, low, biomass; 2- cycles of accrual and sloughing; and 3- seasonal cycles. These patterns predominantly appear to be a result of underlying differences in the hydraulic disturbance regimes among streams.

Relatively constant, low, biomass can occur because of frequent disturbances in streams (e.g., Tett et al. 1978, Biggs and Close 1989). Such disturbances appear to be able to override the effects of other potentially limiting variables such as nutrient availability (e.g., Biggs 1988b, Biggs and Close 1989; although see Lohman et al. 1992). Disturbance of periphyton can result from floods or a streambed dominated by continuously unstable bed sediments. The latter condition is seen frequently in low gradient streams with substrata dominated by sand. However, it is also recognised that relatively constant, low biomass can occur under conditions of very low nutrients and heavy riparian shading (e.g., Lyford and Gregory 1975, Suren

1992). Unfortunately, streams characterised by a high frequency of floods often are also very low in nutrients (e.g., where streams drain highland/alpine and steep forested catchments; Biggs and Close 1989, Close and Davies-Colley 1990). Thus, it is sometimes difficult to separate the importance of disturbance and nutrient availability in determining long-term temporal patterns.

Conversely, perpetually low biomass may be evident where physical disturbance is very infrequent. Such conditions often allow dense invertebrate communities to persist (e.g., Quinn and Hickey 1990), and invertebrate grazing can maintain a low periphyton biomass (e.g., Lamberti and Resh 1983, McAuliffe 1984, Lamberti et al. 1989, Steinman et al. 1991, Power 1992, Biggs and Lowe 1994). This typically occurs in physically stable systems (Winterbourn and Fegley 1989, Winterbourn 1990, Steinman et al. 1991, Biggs and Lowe 1994, Rosemond 1994). The communities in such streams can be dominated for much of the growing season by disturbance - and grazer - resistant taxa including species of *Achnanthidium*, *Cocconeis*, *Cymbella, Synedra* and basal structures of *Stigeoclonium* (Biggs and Gerbeaux 1993, 1994; Biggs and Lowe 1994, Rosemond 1994).

Cycles of accrual and sloughing can be found in streams that experience either moderate frequency of floods or seasonal flood disturbances which temporarily cause major increases in losses over gains (Fig. 1.1, 1.3) (e.g. Uehlinger 1991). Extended periods of flow stability between floods (4 - 10 weeks) allow the accumulation of biomass (e.g., Douglas 1958, Biggs 1988b, Fisher and Grimm 1988, Biggs and Close 1989, Uehlinger 1991, Lohman et al. 1992) with taxonomic structure sometimes proceeding through a succession from diatoms to large green filamentous periphyton and cyanobacteria (Fisher et al. 1982). It should be noted that not every flood results in total biomass loss (Fig. 1.3). Incomplete removal is more likely to occur if the event has only a low intensity, where pre-flood periphyton biomass is low, or the

resident taxa are highly scour resistant (Power and Stewart 1987, Biggs and Close 1989, Grimm and Fisher 1989, Peterson and Stevenson 1992).

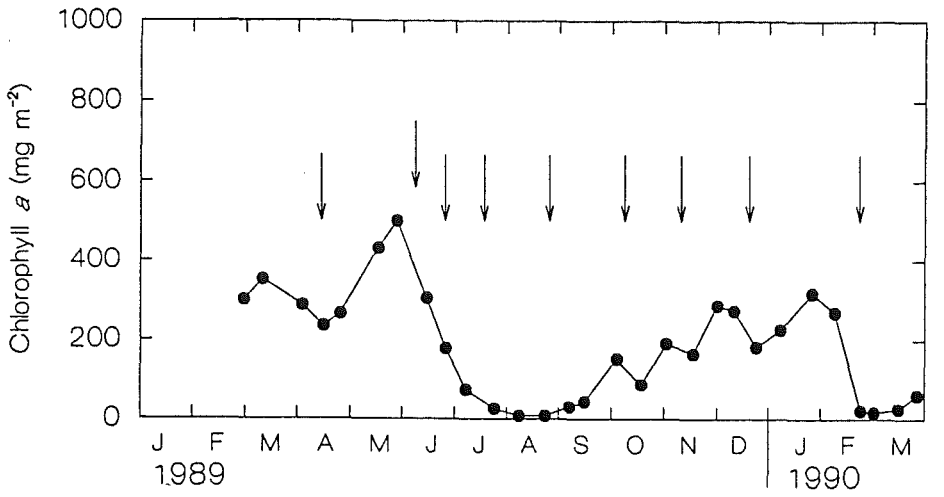


Figure 1.3: A pattern of accrual and sloughing in periphyton communities of the Necker River, Switzerland (data averaged from 10 sites). Arrows indicate flood events (modified from Uehlinger 1991).

Often in gravel/cobble bed streams there may be a window of time immediately after a major flood when invertebrate grazer densities are still low (probably due to slow invertebrate re-colonization and reproduction) (Power 1992). At such times, periphyton accumulation can proceed largely unconstrained by grazing allowing high biomass to develop. However, with increasing time from the last disturbance, losses due to both grazing (Power 1992), and autogenic sloughing (e.g., Biggs and Close 1989), can become significant. Eventually, grazing may be the predominant controller of accrual (Fig. 1.1) (Fisher and Grimm 1991, Power 1992). Thus, there appears to be a shift from 'abiotic' to 'biotic' control of biomass until a further flood re-sets the sequence. Fisher and Grimm (1991) and Power (1992) proposed graphical models of these dynamics (Fig. 1.4 a,b). A large number of streams in both temperate and desert climatic zones (commonly with low to moderate enrichment and draining areas of moderate relief) appear to display the cycles of growth and sloughing (e.g., Douglas 1958, Tett et al. 1978, Jones et al. 1984, Power and Stewart

1987, Biggs 1988ab, Biggs and Close 1989, Grimm and Fisher 1989, Uehlinger 1991, Lohman et al. 1992). A shift from abiotic to biotic control of periphyton biomass late in the accrual cycle has yet to be demonstrated in many streams, however.

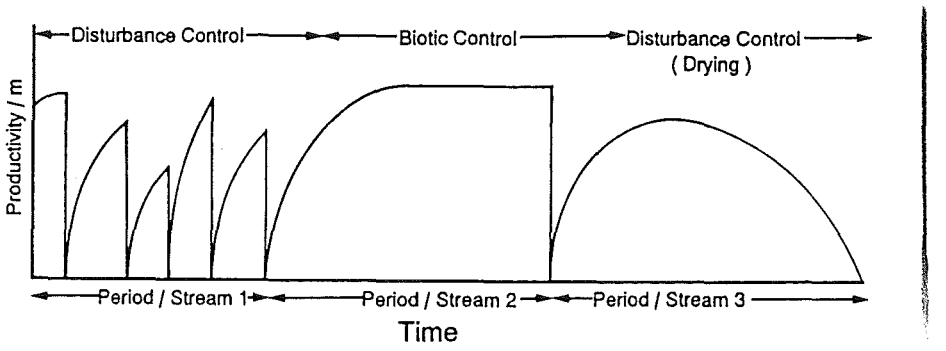


Figure 1.4a: Conceptual model of temporal shift in control of ecosystem functioning influenced by flash flooding. The dependent variable is productivity per linear metre. At times, or in streams, where floods are frequent (Period/Stream 1), hydraulic disturbance-related variables are influential in shaping ecosystem structure and functioning. When or where flow is more stable (Period/Stream 2), biotic interactions control ecosystems (after Fisher and Grimm 1991).

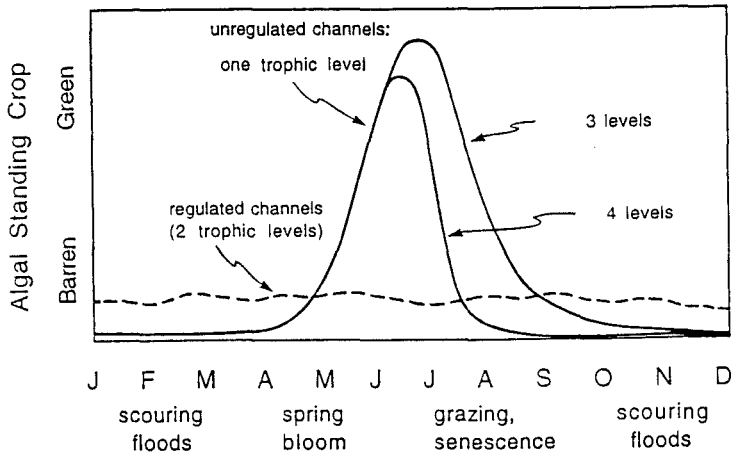


Figure 1.4b: Predicted patterns of seasonal fluctuation in periphyton biomass produced by interactions of hydraulic disturbance and trophic control in regulated and unregulated streams. One trophic level is periphyton only, two levels are composed of periphyton + grazers, three levels are periphyton + grazers + grazer predators (e.g., fish), four levels are periphyton + grazers + grazer predators + larger secondary predators (birds, humans etc) (after Power 1992).

Strong seasonal patterns in community development (Fig. 1.5) appear to be most frequently mediated by a) seasonality in disturbance regimes (providing there are adequate nutrient resources), b) seasonality in grazer activity (where flood disturbances are rare), or c) seasonality in light regimes (where neither disturbance nor grazing are important). For dynamics controlled by seasonality of flow,

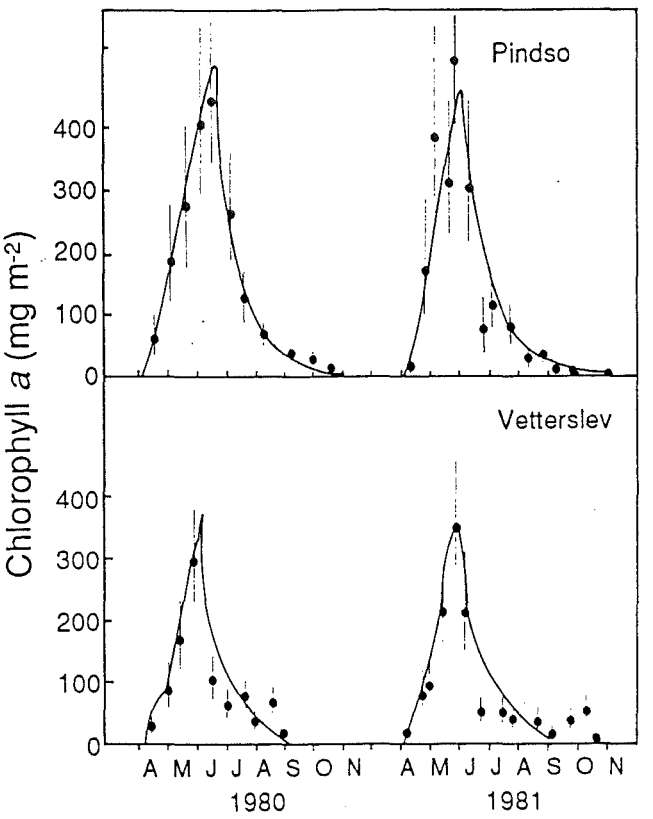


Figure 1.5: Chlorophyll *a* in two stable flowing streams in Denmark over two years showing strong seasonal growth responses. Observed chlorophyll biomass is represented by the dots (plus 95% confidence limits) and the solid line is the predicted biomass using an empirically derived model based on light (from Sand-Jensen et al. 1988).

accumulation of organic matter commences after the last late winter/early spring floods (for example) with the development of diatom dominated communities (e.g., *Diatoma, Synedra, Navicula*). As with short-term periphyton dynamics, communities often become dominated by cyanobacteria in early summer (e.g.,

*Phormidium, Homeothrix*), and patchy growths of large filamentous periphyton such as *Vaucheria* and *Cladophora* in late summer (e.g., Marker 1976, Power 1992). By autumn, much of the biomass in these streams may have degraded and been washed away (Power 1992). Such seasonal dynamics typically occur in enriched spring-fed and lowland streams (e.g., Moore 1977a, Sand-Jensen et al. 1988), those in Mediterranean climatic zones (e.g., Power 1992, Sabater and Sabater 1992) and tropical/subtropical streams (e.g., Necchi and Pascoaloto 1993).

In some stable streams, a seasonal biomass maximum occurs in spring (e.g., Marker 1976, Moore 1977b, Sand-Jensen et al. 1988, Shamsudin and Sleigh 1994), late summer or both (e.g., Biggs and Close 1989). Diatoms tend to dominate communities in spring, whereas filamentous cyanobacteria and/or green periphyton may dominate in late summer (Moore 1977a). As in streams with cycles of accrual and sloughing, periphyton communities can also experience a window of time during early spring when accumulation proceeds largely unchecked by herbivory because of low invertebrate activity in the cold waters (e.g., Power 1992). Thus, it is possible for seasonality in grazing activity to also play an important role in seasonal dynamics of periphyton (Shamsudin and Sleigh 1994).

Some periphyton taxa appear to have autogenic requirements that can limit their development to stable flow periods in specific seasons. These taxa include *Cladophora, Spirogyra, Drapenaldia, Batrachospermum, Gomphonema olivaceum* and *Diatoma vulgare* (see Hynes 1970 for further discussion).

## III. Spatial Patterns

Spatial patterns in the distribution of stream periphyton occur over a wide range of scales; from single grains of sand (e.g., Krejci and Lowe 1986) to entire continents (Sheath and Cole 1992). As with temporal patterns, hydraulic disturbance appears to be an important variable determining spatial patterns (Fig. 1.1).

*Micro-scale: Substratum Patterns*

At the finest level of resolution, periphyton taxa can show preferences for sand grains of different mineralogy and topography. Some stalked diatoms (e.g., *Fragilaria leptostauron*) appear more commonly on "hills" on the surface of stable grains. In contrast, some prostrate diatoms (e.g., *Achnanthidium lanceolata*) inhabit depressions and crevices on grains where they obtain protection from abrasion as grains roll about (Krejci and Lowe 1986).

A common distributional pattern for periphyton in streams during stable flows is for higher biomass to occur on larger substrata (e.g., McConnell and Sigler 1959, Tett et al. 1978, Biggs and Shand 1987) due predominantly to their higher stability during floods (Uehlinger 1991). Zonation in community structure may also occur with increasing depth on boulders (Blum 1956). Most taxa are able to colonize most sizes of substrata and most kinds of material, but can develop into mature communities only if there is a sufficiently long period of habitat stability. Small and medium sized floods (which can occur quite frequently in temperate streams; Biggs and Close 1989) often mobilise fine sediments which then abrade resident communities. However, some periphyton communities can survive on large, stable, particles that protrude above the level of most of the tumbling particles (e.g., Uehlinger 1991). Such communities may achieve a high biomass, whereas those on mobile sands and gravels are more frequently set back to low biomass, early successional stages (e.g., Fisher et

al. 1982). Such processes can result in extremely patchy distributions of periphyton during stable flows (e.g. Power and Stewart 1987).

In some low gradientsstreams with few gravels/cobbles, regular movement of sand substrata maintains a low biomass. In such situations, isolated stable bedrock/boulders may support up to 15-times higher biomass than unconsolidated sand/silt (Biggs and Shand 1987). If patches of silts and sands do stabilize for prolonged periods, then a succession of taxa may occur. First, diatoms can colonize individual particles, but it is rare for them to attain high biomass (e.g., Stevenson and Hashim 1989) since they increase the drag on particles de-stabilizing them. Eventually, cyanobacterial mats may develop over the diatoms, their prostrate filaments binding the surficial layers of silt/sand particles so significant biomass may be achieved (Biggs and Shand 1987).

*Meso-scale: Within Catchment Patterns*

Differences in biomass and species composition can occur between pool, run and riffle habitats of unshaded streams, these differences apparently reflecting spatial differences in shear stress, nutrient mass transfer and substratum type (size and disturbance history, Fig. 1.1 and see preceeding section). There is little published data on patterns in periphyton accrual among these habitats, but it appears that opposite responses can exist depending on whether the water is enriched or not (my unpublished observations). In enriched streams, high biomass communities often develop in low-velocity runs and pools. They are usually dominated by filamentous green periphyton (e.g., *Spirogyra, Oedogonium, Cladophora*), whereas in riffles higher shear stresses restrict the maximum thickness of the periphyton mat (and thus biomass) compared with that in pools. Thus, in riffles communities are often dominated by low growing diatoms (e.g., *Cocconeis, Cymbella, Nitzschia*) (e.g., see Peterson and Stevenson 1990, Poff et al. 1990 for experimental data on community develoment as a function of velocity). In contrast, in unenriched streams the highest

periphyton biomass (dominated by diatoms) is usually encountered in high velocity riffles (e.g., Scarsbrook and Townsend 1993). This is probably a consequence of increased mass transfer of metabolites at higher velocities and with greater turbulence (e.g., Whitford and Schumacher 1964, Lock and John 1979, Raven 1992, Stevenson and Glover 1993, Borchardt 1994).

The River Continuum Concept (RCC; Vannote et al. 1980) proposed that a downstream pattern of increasing periphyton biomass should occur from headwater to mid-catchment reaches as streams coalesce, the channel becomes wider, and riparian shading is reduced. Biomass is predicted to decrease again in the lower regions as a function of increasing light attenuation with greater water depths and increased turbidity. This proposed pattern is intuitively correct in catchments with forested headwaters and has been verified in a number of streams at certain times of the year (e.g., Minshall et al. 1983). However, localized features of habitats can often interrupt such downstream trends. In some catchments where the headwater regions are developed for agriculture, the RCC pattern can be reversed (Wiley et al. 1990), whereas in catchments with frequent floods and/or localized nutrient inputs, periphyton communities may display quite different patterns because of the overiding effects of these variables at catchment and local scales (e.g., Sabater and Sabater 1992). In determining whether the distribution of periphyton in a stream should conform to the RCC pattern, it is important to recognize the influence of downstream changes in channel geometry. The classical geomorphic model describes a pattern of decreasing bed gradient, widening of the active channel and a decrease in substratum particle size moving downstream (e.g., Vannote et al. 1980). This results in a progressive reduction in hydraulic stress (Brussock et al. 1985, Statzner and Higler 1986, Statzner et al. 1988). However, in regions with complex geology and tectonic activity, major discontinuities in catchment gradient can occur, and these can impose strong, localized, hydraulic constraints on periphyton development (Biggs 1990b). Other localised controls include canopy cover and tributary inputs. Such constraints

can easily mask the straight forward downstream trends as proposed in the RCC (e.g., Biggs and Gerbeaux 1993).

In many catchments (particularly those with little forest cover) a downstream increase in nutrient loading can be expected and this should lead to gradients in community composition and biomass. Headwater reaches are frequently dominated by diatoms (e.g., *Cymbella, Gomphoneis, Fragilaria*), cyanobacteria (e.g., *Schizothrix, Phormidium*), red algae (Rhodophyceae) (e.g., *Batrachospermum* sp.), and several low biomass filamentous green taxa (e.g., *Stigeoclonium*). As enrichment increases down the catchment (e.g., with higher intensity landuse), nutrient demanding taxa such as the filamentous chrysophyte *Vaucheria* sp., and the filamentous green alga *Cladophora glomerata*, often become more prominent and can achieve high biomass (e.g., Holmes and Whitton 1981, Entwistle 1989).

*Broad Scale: Inter-catchment Patterns*

An extremely wide range of periphyton biomass and community composition is possible among streams. This variability reflects spatial differences in broad environmental features of regions (termed 'primary' or 'ultimate' variables; Biggs et al. 1990, Naiman et al. 1992) which inturn control the local resources, disturbance and grazing (Fig. 1.1) (termed 'secondary' or 'proximate' variables: Biggs et al. 1990, Naiman et al. 1992). A fundamental broad scale pattern in periphyton biomass and community composition can be the result of differences in the frequency of flood events among streams. In accordance with the previous discussion, streams which experience frequent hydraulic disturbances tend to have low average biomass (Tett et al. 1978, Biggs and Close 1989), with communities dominated by low growing, highly shear-resistant, taxa (e.g., Luttenton and Rada 1987, Robinson and Rushforth 1987). Conversely, more benign habitats (these having long time intervals between disturbances, little resource stress and no heavy grazing) tend to have communities

with higher biomass and greater architectural complexity (e.g., Biggs and Price 1987, Biggs 1990b).

Differences in community composition and biomass among regions during periods of low flow may reflect regional differences in geology/landuse and associated enrichment (e.g., Biggs 1990b, Biggs et al. 1990, Biggs and Gerbeaux 1993, Leland 1995). Green algae such as *Ulothrix zonata*, *Stigeoclonium* sp., *Spirogyra* sp., and the cyanobacterium *Phormidium* sp. often form communities of low biomass in unenriched streams (Fig. 1.6). However, in enriched streams periphyton communities are usually dominated by large filamentous taxa such as *Cladophora glomerata* and *Rhizoclonium* sp. which attain a high biomass.

As can be anticipated from the earlier discussion, there is also a strong interaction between disturbance and enrichment in determining large scale spatial patterns. It is likely that a combination of infrequent flood disturbances and high levels of enrichment are necessary to attain a high average monthly biomass (e.g., > 100 mg $m^{-2}$ chlorophyll *a*) of periphyton in streams. Conversely, if flood disturbances are very frequent, and/or levels of enrichment are very low, mean monthly biomass will be low. High levels of enrichment result in some periphyton accrual at high frequencies of disturbance because of more rapid inter-flood regeneration, and some biomass can also accrue with low levels of enrichment providing that disturbance frequency is also low.

Among streams on the North American continent, there is a tendency for filamentous chrysophytes to decrease in abundance (except in the tundra biome) and for red algae to increase as latitude decreases (Sheath and Cole 1992). No pattern is evident, however, for cyanobacteria. The boreal forest biome has the highest species richness and the tundra/desert-chaparal biomes have the lowest. In terms of biome similarities, macroalgal communities in the boreal and western conifer biomes are

very similar, with the eastern hemlock-hardwood forest and deciduous forest biomes also having floras that are moderately similar (Sheath and Cole 1992).

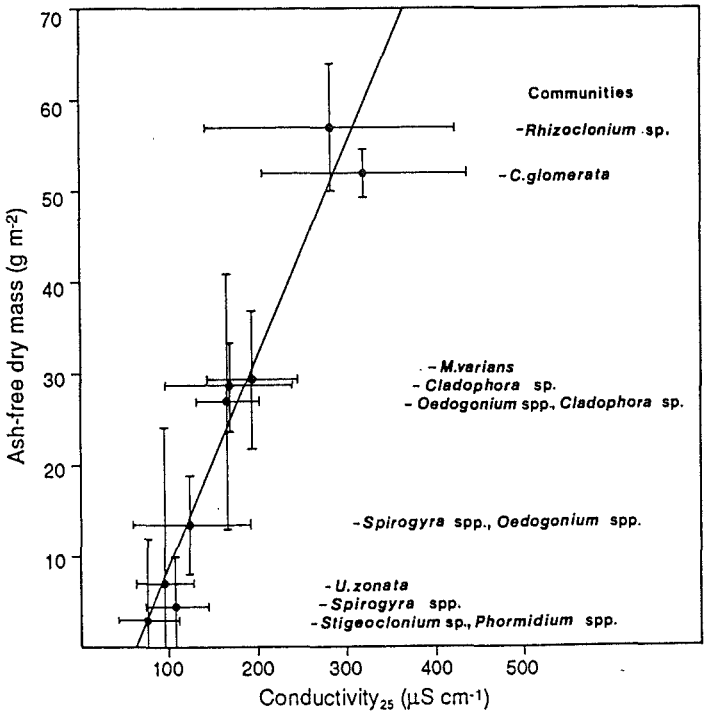


Figure 1.6: Relationship between mean AFDM biomass for nine different periphyton communities and conductance of the water (a relative measure of enrichment) from a survey of over 400 New Zealand streams during summer low flows. The error bars are 1 S.D. (*C. glomerata* = *Cladophora glomerata, M. varians* = *Melosira varians, U. zonata* = *Ulothrix zonata*) (modified from Biggs and Price 1987).

## IV. Periphyton Proliferations

Excessive accumulations of periphyton in streams at the peak of the accrual cycle are a widespread phenomenon (e.g., Wharfe et al. 1984, Biggs 1985a, Biggs and Price 1987, Welch et al. 1989, Chessman et al. 1992). They can potentially affect abstraction for water supply, aesthetic appeal and instream recreation. They can also degrade ecosystem structure. Most severe cases occur under high nutrient loadings,

which may originate from areas of nutrient rich rocks, intensive agricultural development, and/or nutrient-rich waste discharges.

Filamentous green periphyton such as *Ulothrix* (in cold waters), *Cladophora* and *Rhizoclonium* usually present the greatest nuisance. In less enriched streams, stalked and tube dwelling diatoms such as species of Gomphonemaceae (e.g., *Gomphoneis herculeana* and *Didymosphenia geminata*) and Cymbellaceae (e.g., *Cymbella affinis*) can also be a problem (e.g., Biggs and Price 1987). These periphyton groups form very different macroscopic communities. Green periphyton develop streaming beds of filaments which can be up to several meters long in low velocity areas, and often detach and float near the surface (e.g., Power 1990). These floating mats can then become entangled in branches or around cobbles protruding from the bottom of the stream, and they often continue to proliferate on them. In contrast, diatoms tend to form thick gelatinous mats which consist predominantly of polysaccharides (Hoagland et al. 1993). Diatom mats may attain a thickness of a centimetre or more, they may completely smother the substrata, and in some streams they can strongly resemble whitish-grey sewage fungus.

What constitutes a nuisance growth is not always clear because specific criteria need to be established for specific water uses. As an initial guide for the control of proliferations, Horner et al. (1983) suggested that chlorophyll *a* > 100-150 mg $m^{-2}$ is unacceptable. While surveying over 400 streams in New Zealand, Biggs and Price (1987) observed that when in excess of 40% of the bed was covered by filamentous periphyton the community became very conspicuous from the bank. They also observed that if biomass was > 50 g $m^{-2}$ AFDM (approximately 55% cover) it usually resulted in extensive smothering of bed sediments. From a literature review of biomass values in various habitats, Nordin (1985) recommended the following periphyton biomass criteria for streams of British Columbia, Canada: < 50 mg $m^{-2}$ chlorophyll *a* to protect recreational usage, and < 100 mg $m^{-2}$ to protect other aquatic

life. Similarly, in New Zealand, the Ministry for the Environment (MfE 1992) has recommended to water management agencies that to protect contact recreational usage of streams, the seasonal maximum cover by filamentous periphyton should not exceed 40%, and/or biomass should not exceed 100 mg $m^{-2}$ chlorophyll *a* or 40 g $m^{-2}$ AFDM. The existence of these guidelines demonstrates that the control of undesirable periphyton growths in streams is becoming an important water management issue.

## V. Concluding Remarks

A complex array of factors and interactions govern the development of periphyton communities in streams, and the competitive success of any one species is difficult to predict. Periphyton have high turnover and opportunistic life history strategies which have enabled them to successfully exploit stream habitats, many of which are harsh environments. However, clear patterns in biomass and community structure do exist. These patterns can be explained in general terms as being both interacting and separate functions of gradients in accrual (nutrient and light resources) and loss (disturbance and grazing), variables which operate over small to large spatial scales, and for periods from weeks to years.

## VI . References

Barnese L.E. & Lowe R.L. (1992) Effects of substrate, light, and benthic invertebrates on algal drift in small streams. *Journal of the North American Benthological Society*, **11**, 49-59.

Biggs B.J.F. (1985a) Algae: a blooming nuisance in rivers. *Soil and Water*, **21**, 27-31.

Biggs B.J.F. (1985b) The use of periphyton in the monitoring of water quality. *Biological Monitoring in Freshwaters: proceedings of a seminar* (Eds. R.D. Pridmore & A.B. Cooper), pp. 117-142. Biological Monitoring in Freshwaters: proceedings of a seminar, Ministry of Works and Development.

Biggs B.J.F. (1988a) Artificial substrate exposure times for periphyton biomass estimates in rivers. *New Zealand Journal of Marine and Freshwater Research*, **22**, 189-199.

Biggs B.J.F. (1988b) Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1405-1411.

Biggs B.J.F. (1989) Biomonitoring of organic pollution using periphyton. South Branch, Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **23**, 263-274.

Biggs B.J.F. (1990a) Use of relative specific growth rates of periphytic diatoms to assess enrichment of a stream. *New Zealand Journal of Marine and Freshwater Research*, **24**, 9-18.

Biggs B.J. (1990b) Periphyton communities and their environments in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 367-386.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs B.J.F., Duncan M.J., Jowett I.G., Quinn J.M., Hickey C.W., Davies-Colley R.J. & Close M.E. (1990) Ecological characterisation, classification and modelling of

New Zealand rivers: an introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research*, **24**, 277-304.

Biggs B.J.F. & Gerbeaux P. (1993) Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **27**, 39-53.

Biggs B.J.F. & Gerbeaux P.J. (1994) Epilithic periphyton in temperate rivers: community composition in relation to differences in disturbance regimes. *NIWA-Christchurch Miscellaneous Report*, **177**, 33.

Biggs B.J.F. & Lowe R.L. (1994) Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *New Zealand Journal of Marine and Freshwater Research*, **28**, 119-134.

Biggs B.J.F. & Price G.M. (1987) A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **21**, 175-191.

Biggs B.J.F. & Shand B.I. (1987) *Biological communities and their potential effects of power developments in the Lower Clutha River, Otago*. Ministry of Works and Development. 127p.

Blum J.L. (1956) The ecology of river algae. *The Botanical Review*, **2**, 291-341.

Borchardt M.A. (1994) Effects of flowing water on nitrogen- and phosphorus-limited photosynthesis and optimum N:P ratios by *Spirogyra fluviatilis* (Charophyceae). *Journal of Phycology*, **30**, 418-430.

Boston H.L. & Hill W.R. (1991) Photosynthesis-light relations of stream periphyton communities. *Limnology and Oceanography*, **36**, 644-656.

Bothwell M.L. (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1293-1301.

Bothwell M.L., Suzuki K.E., Bolin M.K. & Hardy F.J. (1989) Evidence of dark avoidance by phototrophic periphytic diatoms in lotic systems. *Journal of Phycology*, **25**, 85-94.

Brussock P.P., Brown A.V. & Dixon J.C. (1985) Channel form and stream ecosystem models. *Water Resources Bulletin*, **21**, 859-866.

Cattaneo A., Ghittori S. & Vendegna V. (1975) The development of benthonic phytocoenosis on artificial substrates in the Ticino River. *Oecologia*, **19**, 315-327.

Chessman B.C., Hutton P.E. & Burch J.M. (1992) Limiting nutrients for periphyton growth in sub-alpine, forest, agricultural and urban streams. *Freshwater Biology*, **28**, 349-361.

Close M.E. & Davies-Colley R.J. (1990) Baseflow water chemistry in New Zealand rivers. 2. Influence of environmental factors. *New Zealand Journal of Marine and Freshwater Research*, **24**, 343-356.

Dodds W.K. (1989) Photosynthesis of two morphologies of *Nostoc parmelioides* (Cyanobacteria) as related to current velocities and diffusion patterns. *Journal of Phycology*, **25**, 258-262.

Dodds W.K. (1991) Micro-environmental characteristics of filamentous algal communities in flowing freshwaters. *Freshwater Biology*, **25**, 199-209.

Douglas B. (1958) The ecology of the attached diatoms and other algae in a stony stream. *Journal of Ecology*, **46**, 295-322.

Downes B.J., Lake P.S. & Schreiber E.S.G. (1993) Spatial variation in the distribuiton of stream invertebrates: implications of patchiness for models of community organization. *Freshwater Biology*, **30**, 119-132.

Entwistle T.J. (1989) Macroalgae in the Yarra River Basin: Flora and Distribution. *Proceedings of the Royal Society of Victoria*, **101**, 1-76.

Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monograph*, **52**, 93-110.

Fisher S.G. & Grimm N.B. (1988) Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1183-1190.

Fisher S.G. & Grimm N.B. (1991) Streams and disturbance: are cross-ecosystem comparisons useful? *Comparative analyses of ecosystems-patterns, mechanisms and theories* (Eds. J. Cole, G. Lovett & S. Findlay), pp. 196-221. Comparative analyses of ecosystems-patterns, mechanisms and theories, Springer-Verlag.

Grimm N.B. & Fisher S.G. (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, **8**, 292-307.

Hill W.R. & Knight A.W. (1988) Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology*, **24**, 125-132.

Hoagland K.D., Rosowski J.R., Gretz M.R. & Roemer S.C. (1993) Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. *Journal of Phycology*, **29**, 537-566.

Holmes N.T.H. & Whitton B.A. (1981) Phytobenthos of the River Tees and its tributaries. *Freshwater Biology*, **11**, 139-168.

Horner R.R., Welch E.B., Seeley M.R. & Jacoby J.M. (1990) Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology*, **24**, 215-232.

Horner R.R., Welch E.B. & Veenstra R.B. (1983) Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. *Periphyton of Freshwater Ecosystems* (Ed. R.G. Wetzel), pp. 121-134. Periphyton of Freshwater Ecosystems, Junk.

Hudon C. & Bourget E. (1981) Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1371-1384.

Hynes H.B.N. (1970) *The Ecology of Running Waters*. University of Toronto Press.

Jones J.R., Smart M.M. & Burroughs J.N. (1984) Factors related to algal biomass in Missouri Ozark streams. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **22**, 1867-1875.

Jones R.C. (1978) Algal biomass dynamics during colonization of artificial islands: experimental results and a model. *Hydrobiologia*, **59**, 165-180.

Kaufman L.H. (1979) Stream aufwuchs accumulation processes: effects of ecosystem de-population. *Hydrobiologia*, **70**, 75-81.

Kjeldsen K. (1994) The relationship between phosphorus and peak biomass of benthic algae in small lowland streams. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **25**, 1530-1533.

Korte V.L. & Blinn D.W. (1983) Diatom colonization of artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *Journal of Phycology*, **19**, 332-341.

Krecji M.E. & Lowe R.L. (1986) Importance of sand grain mineralogy and topography in determining micro-spatial distribution of epipsammic diatoms. *Journal of the North American Benthological Society*, **5**, 211-220.

Lamberti G.A., Gregory S.V., Ashkenas L.R., Steinman A.D. & McIntire C.D. (1989) Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology*, **70**, 1840-1856.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores; experimental study of grazing by a caddisfly population. *Ecology*, **64**, 1124-1135.

Leland H. (1995) Distribution of phytobenthos in the Yakima River Basin, Washington, in relation to geology, land use and other environmental factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, in press.

Lock M.A. (1979) Notes. The effect of flow patterns on uptake of phosphorus by river periphyton. *Limnology and Oceanography*, **24**, 376-383.

Lock M.A. (1981) River epilithon-a light and organic energy transducer. *Perspectives in running Water Ecology* (Eds. M.A. Lock & D.D. Williams), pp. 3-40. Perspectives in running Water Ecology, Plenum Press.

Lohman K., Jones J.R. & Perkins B.D. (1992) Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1198-1205.

Lowe R.L., Golladay S.W. & Webster J.R. (1986) Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *Journal of the North American Benthological Society*, **5**, 221-229.

Luttenton M.R. & Rada R.G. (1986) Effects of disturbance on epiphytic community architecture. *Journal of Phycology*, **22**, 320-326.

Lyford J.H. Jr. & Gregory S.V. (1975) The dynamics and structure of periphyton communities in three Cascade Mountain streams. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **18**, 1610-1616.

Marker A.F.H. (1976) The benthic algae of some streams in southern England. *Journal of Ecology*, **64**, 343-358.

McAuliffe J.R. (1984) Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. *Oikos*, **42**, 327-333.

McColl R.H.S. (1974) Self-purification of small freshwater streams: phosphate, nitrate, and ammonia removal. *New Zealand Journal of Marine and Freshwater Research*, **8**, 375-388.

McConnell W.J. & Sigler W.F. (1959) Chlorophyll and productivity in a mountain river. *Limnology and Oceanography*, **4**, 335-351.

McCormick P.V. & Cairns J. (1994) Algae as indicators of environmental change. *Journal of Applied Phycology*, **6**, 509-526.

MfE (1992) *Water Quality Guidelines No. 1: Guidelines for the control of undesirable biological growths in water*. New Zealand Ministry for the Environment. 60p.

Minshall G.W. (1978) Autotrophy in stream ecosystems. *BioScience*, **28**, 767-771.

Minshall G.W., Petersen R.C., Cummins K.W., Bott T.L., Sedell J.R., Cushing C.E. & Vannote R.L. (1983) Interbiome comparison of stream ecosystem dynamics. *Ecological Monograph*, **53**, 1-25.

Moore J.W. (1977) Seasonal succession of algae in a eutrophic stream in Southern England. *Hydrobiologia*, **53**, 181-192.

Moore J.W. (1977) Some factors effecting algal densities in a eutrophic farmland stream. *Oecologia*, **29**, 257-267.

Mulholland P.J., Steinman A.D., Palumbo A.V. & DeAngelis D.L. (1991) Influence of nutrients and grazing on the response of stream periphyton communities to a scour disturbance. *Journal of the North American Benthological Society*, **10**, 127-142.

Naiman R.J., Longzarich D.G., Beechie T.J. & Ralph S.C. (1992) *General principles of classification and the assessment of conservation potential in rivers*. John Wiley and Sons Ltd. 470p.

Necchi O.J. & Pascoaloto D. (1993) Seasonal dynamics of macroalgal communities in the Preto River basin, Sao Paulo, southeastern Brazil. *Archiv fur Hydrobiologie*, **129**, 231-252.

Nordin R.N. (1985) *Water quality criteria for nutrients and algae (technical appendix)*. Water Quality Unit, Resource Quality Section, Water Management Branch, British Columbia Ministry for the Environment, Victoria. 104p.

Oemke M.P. & Burton T.M. (1986) Diatom colonization dynamics in a lotic system. *Hydrobiologia*, **139**, 153-166.

Osborne L.L. (1983) Colonization and recovery of lotic epilithic communities: a metabolic approach. *Hydrobiologia*, **99**, 29-36.

Peterson C.G. & Stevenson R.J. (1990) Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Botany*, **68**, 2092-2102.

Peterson E.G. & Stevenson R.J. (1992) Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*, **73**, 1445-1461.

Poff N.L., Voelz N.J. & Ward J.V. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society*, **9**, 303-318.

Power M.E. (1990) Benthic turfs vs floating mats of algae in river food webs. *Oikos*, **58**, 67-79.

Power M.E. (1992) Hydrological and trophic controls of seasonal algal blooms in northern California rivers. *Archiv fur Hydrobiologie*, **125**, 375-410.

Power M.E. & Stewart A.J. (1987) Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist*, **117**, 333-345.

Quinn J.M. & Hickey C.W. (1990) Magnitude of effects of substrate particle size, recent flooding and catchment development on benthic invertebrate communities in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 411-427.

Raven J.A. (1992) How benthic macroalgae cope with flowing freshwater resource acquisition and retention. *Journal of Phycology*, **28**, 133-146.

Reiter M.A. (1989) The effect of a developing algal assemblage on the hydrodynamics near substrates of different sizes. *Archiv fur Hydrobiologie*, **115**, 221-244.

Robinson C.T. & Rushforth S.R. (1987) Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiologia*, **154**, 49-59.

Rosemond A.D. (1994) Multiple factors limit seasonal variation in periphyton in a forest stream. *Journal of the North American Benthological Society*, **13**, 333-344.

Rosemond A.D., Mullholland P.J. & Elwood I.W. (1993) Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology*, **74**, 1264-1280.

Sabater S. & Sabater R. (1992) Longitudinal changes of benthic algal biomass in a mediterranean river during two high production periods. *Archiv fur Hydrobiologie*, **124**, 475-487.

Sand-Jensen K., Moller J. & Olesen B.H. (1988) Biomass regulation of microbenthic algae in Danish lowland streams. *Oikos*, **53**, 332-340.

Scarsbrook M.R. & Townsend C.R. (1993) Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Scrimgeour G.J., Davidson R.J. & Davidson J.M. (1988) Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, **22**, 337-344.

Shamsudin L. & Sleigh M.A. (1994) Seasonal changes in composition and biomass of epilithic algal floras of a chalk stream and a soft water stream with estimates of production. *Hydrobiologia*, **273**, 131-146.

Sheath R.G. & Cole K.M. (1992) Biogeography of stream macroalgae in North America. *Journal of Phycology*, **28**, 448-460.

Statzner B., Gore J.A. & Vincent H.R. (1988) Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, **7**, 307-360.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology*, **16**, 127-139.

Steinman A.D., Mulholland P.J. & Kirschitel D.B. (1991) Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure and P uptake in lotic periphyton communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1951-1959.

Stevenson R.J. (1983) Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. *Ecology*, **64**, 1514-1524.

Stevenson R.J. (1986) Importance of variation in algal immigration and growth rates estimated by modelling benthic algal colonization. *Algal Biofouling* (Eds. L.V. Evans & K.D. Hoagland), pp. 193-210. Algal Biofouling, Elsevier.

Stevenson R.J. (1990) Benthic algal community dynamics in a stream during and after a spate. *Journal of the North American Benthological Society*, **9**, 277-288.

Stevenson R.J. & Glover R. (1993) Effects of algal density and current on ion transport through periphyton communities. *Limnology and Oceanography*, **38**, 1276-1281.

Stevenson R.J. & Hashim S. (1989) Variation in diatom community structure among habitats in sandy streams. *Journal of Phycology*, **25**, 678-686.

Stevenson R.J. & Peterson C.G. (1989) Variation in benthic diatom (*Bacillariophyceae*) immigration with habitat characteristics and cell morphology. *Journal of Phycology*, **25**, 120-129.

Stevenson R.J. & Peterson C.G. (1991) Emigration and immigration can be important determinants of benthic diatom assemblages in streams. *Freshwater Biology*, **26**, 279-294.

Suren A.M. (1992) Enhancement of invertebrate food resources by bryophytes in New Zealand alpine headwater streams. *New Zealand Journal of Marine and Freshwater Research*, **26**, 229-239.

Tett P., Gallegos C., Kelly M.G., Hornberger G.M. & Cosby B.J. (1978) Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. *Limnology and Oceanography*, **23**, 785-797.

Trotter D.M. & Hendricks A.C. (1979) Attached, filamentous algal communities. *Methods and Measurements of Periphyton Communities: a review* (Ed. R.L. Weitzel), pp. 58-69. Methods and Measurements of Periphyton Communities: a review, American Society for Testing Materials.

Uehlinger U. (1991) Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv fur Hydrobiologie*, **123**, 219-237.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.

Vymazal J. (1988) The use of periphyton communities for nutrient removal from polluted streams. *Hydrobiologia*, **166**, 225-237.

Welch E.B., Horner R.R. & Patmont C.R. (1989) Prediction of nuisance periphytic biomass: a management approach. *Water Research*, **23**, 401-405.

Wharfe J.R., Taylor K.S. & Montgomery H.A.C. (1984) The growth of *Cladophora glomerata* in a river receiving sewage effluent. *Water Research*, **18**, 971-979.

Whitford L.A. & Schumacher G.J. (1964) Effect of a current of respiration and mineral uptake in *Spirogyra* and *Oedogonium*. *Ecology*, **45**, 168-170.

Whitton B.A. (1975) Algae. *River Ecology* (Ed. B.A. Whitton), pp. 81-105. River Ecology, University of California Press.

Whitton B.A. (1979) Algae and higher plants as indicators of river pollution. *Biological Indicators of Water Quality* (Eds. A. James & L. Evison), pp. 5-1 to 5-34. Biological Indicators of Water Quality, John Wiley & Sons.

Wiley M.J., Osborne L.L. & Larimore R.W. (1990) Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 373-384.

Winterbourn M.J. (1990) Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology*, **23**, 463-474.

Winterbourn M.J. & Fegley A. (1989) Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, South Island, streams. *New Zealand Natural Sciences*, **16**, 57-65.

# Chapter 2

## The contribution of hydraulic disturbance and nutrient resource supply to the habitat template of periphyton in stream ecosystems

**Preface**

In this chapter average monthly periphyton biomass in a sample of streams is analysed as a function of a gradient in hydraulic disturbance frequency. These disturbance effects are then integrated with measurements of nutrient supply to determine the interaction of disturbance and nutrients as determinants of the habitat template of periphyton in streams. I discussed the general principles and importance of disturbance frequency for periphyton development in Chapter 1, but no studies have quantified disturbance frequency based on mechanistic parameters which can be quantified and modelled simply, nor have they analysed many sites in natural streams covering orthogonal gradients of both disturbance and resource supply. This paper has now been published in *Freshwater Biology* **33**:101-120.

## I. Introduction

For plants in many ecosystems, a number of factors contribute to growth and death, thus affecting biomass dynamics and competitive interactions. Grime (1977) classified these into two categories: resource 'stress'; conditions controlling productivity/cellular growth rates (e.g. shortages of light, mineral nutrients, sub-optimal temperatures); and 'disturbance', short-term physical perturbations in the environment which result in partial or total destruction of plant biomass (e.g. frosts, winds). Such disturbance phenomena can overide or interact with nutrients, competition, and herbivory to regulate productivity and biomass accrual (Pickett & White, 1985; and papers contained therein).

Periphyton (mainly attached algae) are the dominant primary producers in most temperate stream ecosystems. As with plant communities in terrestrial habitats, biomass accrual is essentially dictated by the balance between organic matter gain and loss (Chapter 1, Biggs 1994). Experimental studies have shown that light, nutrients (nitrogen and phosphorus), and temperature are the main variables controlling productivity and biomass gain (e.g. Bothwell, 1988; 1989; Boston & Hill, 1991), whereas disturbance (by flood induced substrate and velocity instability) and invertebrate grazing, are important variables controlling biomass loss (e.g. Lamberti & Resh, 1983; Robinson & Minshall, 1986; Power & Stewart, 1987; Biggs & Close, 1989; Horner *et al.*, 1990; Winterbourn, 1990; Hill *et al.*, 1992).

While much detailed experimental research has been carried out on periphyton growth processes we still do not have the broadscale conceptual understanding to explain inter-biome differences in periphyton among streams. Development of such an understanding would greatly assist translating experimental results to other situations, establish a clearer framework for the management of stream environments, and eventually assist the development of quantitative ecosystem models. As a first step toward this, the proximate variables of disturbance and enrichment need to be depicted in terms of the ultimate properties of catchments such as their climate, geology and landuse (Naiman *et al.*, 1992). Climate dictates the frequency of floods among regions (e.g. Poff & Ward, 1989; Jowett & Duncan, 1990), and catchment geology and landuse dictate levels of enrichment (e.g. Dillon & Kirchner, 1975; Omernik, 1977; Hill, 1978; Cooper *et al.*, 1987; Close & Davies-Colley, 1990).

The objective of this study was to measure periphyton development across geographic regions which encompass wide gradients in climate (controlling disturbance by floods) and geology/landuse (controlling levels of nutrient enrichment). Through this I wished to determine how these variables interact to dictate the average quantity of periphyton that will grow in streams of different regions over a year, and determine how disturbance and enrichment interact in natural systems to form the

habitat template of periphyton. Specifically, I hypothesised that: 1) over a broad range of disturbance regimes, average periphyton biomass should be a negative correlate of disturbance frequency regardless of nutrient resources; and 2) nutrient availability, should be a secondary modifier of the effects of disturbance. Fisher & Grimm (1988) suggested that examination of the structure of stream communities over a spectrum of disturbance regimes would contribute greatly to a worldwide functional geography of lotic ecosystems.

## II. Materials and Methods

*Background: New Zealand stream environments*

Natural stream studies of disturbance and enrichment effects are difficult and costly to achieve in continental regions because of the vast distances between systems of different climatic, geologic and associated landuse regimes. However, New Zealand provides a compact, natural, outdoor laboratory for such studies. Most parts of the land mass are within a belt of strong westerly winds which bring regular, rain-bearing frontal systems. In some areas mountains rise to over 2,500 m above sea-level in less than 25 kilometres. Such conditions have created gradients in annual rainfall from over 12 m to less than 0.35 m in distances of less than 100 km (Griffiths & McSaveney, 1983). Superimposed on these gradients is a complex geological structure composed of nutrient-poor, hard, metamorphosed sedimentary rocks, and plutonic granites together with zones of nutrient-rich Tertiary sand/siltstones of marine origin, and volcanic tephras/bedrocks (Suggate & Riddolls, 1976). Major changes in these rock types often occur over moderate to small spatial scales (< 100 km) and have important effects on stream-water chemistry (e.g. Timperley, 1983; Close & Davies-Colley, 1990; Biggs & Gerbeaux 1993). Associated with this lithological template are major changes in landuse intensity, including intensive dairying, horticulture, cropping, extensive sheep grazing, and undeveloped native tussock grasses. These differences in landuse also result in large differences in stream nutrients over small areas (e.g. Copper *et al.*, 1987; Rutherford *et al.*, 1987; Close & Davies-Colley, 1990). A more comprehensive characterisation of New Zealand streams is given by Biggs *et al.* (1990).

*Site selection criteria*

Flow data were obtained from the New Zealand national water resources archive (administered by the National Institute of Water and Atmospheric Research) and time-flow plots were developed for the most recent 10-year period to determine the average frequency of floods for site selection. Any increase in flow greater than 5 x the average for the preceding 7 days was classified as a flood (after Biggs & Close, 1989). This was later refined to a velocity criterion using data collected at the sites.

Catchment characteristics were obtained by digitising boundaries from 1:63,000 scale topographical maps and overlaying these on a spatial data base of landuse information, the New Zealand Land Resources Inventory, mapped at a resolution of 50 - 60 $m^2$ (Ministry of Works and Development, 1979). This is a GIS type system which enables proportions of catchments in various rock and landuse types to be determined to a precision of less than 1%. For the present analysis, a condensation of the data was carried out to give general rock and landuse groups as follows: hard rocks = greywackes and schist (both fine grained metamorphics) + granites (plutonics) + ultramafics; soft rocks = unconsolidated Tertiary (marine) silt and sandstone; alkaline rocks = limestone + marble; ash = unconsolidated volcanic ash usually underlain by andesites/rhyolites/ignimbrites. Intensity of landuse was defined as follows; high = intensive pastoral development, dairying, cropping and horticulture; moderate = extensive pastoral grazing on exotic pasture grasses or improved native tussock grass, together with commercial forest plantations (generally fertilized); and low = native forest, scrubland, and undeveloped tussock grassland.

One of three 'potential enrichment' designations was pre-assigned to catchments based on their geology/landuse, and the studies of Biggs (1990), Quinn & Hickey (1990), Close & Davies-Colley (1990) and Biggs & Gerbeaux (1993) which have linked broadscale differences in low-flow nutrient levels and periphyton growth in New Zealand streams with certain rock types and degrees of agricultural development. The categories, and arbitrary criteria for each were: nutrient rich = > 40% composed of soft + alkaline + ash rock + high intensity landuse; moderately enriched = 20 - 40 % soft + alkaline + ash rock + high intensity landuse and/or > 80 % moderate intensity landuse; and nutrient poor = < 20 % soft + alkaline + ash rock + high intensity landuse.

The classification of potential enrichment was combined with estimates of disturbance frequency to achieve a final set of 16 sites in 12 catchments (Fig. 2.1). A summary of the sites, their flow and flood regime statistics, and their catchment characteristics is given in Tables 2.1 and 2.2. While combinations of high/intermediate frequency disturbance and low nutrient status catchments were easily achieved, it was difficult to find sites with low frequency disturbances having low nutrient status catchments. This was because in climatic zones with a low frequency of heavy rain events there was generally little forest cover, high agricultural development, and/or much soft, nutrient-rich, rock. Indeed, agricultural development is usually concentrated in regions where hours of sunshine and soil fertility are highest. Thus, only a partial cross gradient in flood frequency and enrichment could be achieved.

*Field procedures*

Flows were monitored at all but three sites using Foxboro, or pressure transducer, water level recorders. Rating curves were developed based on numerous gaugings which covered a full range of flows. Gaugings were also carried out at least monthly by DSIR/NIWA field teams

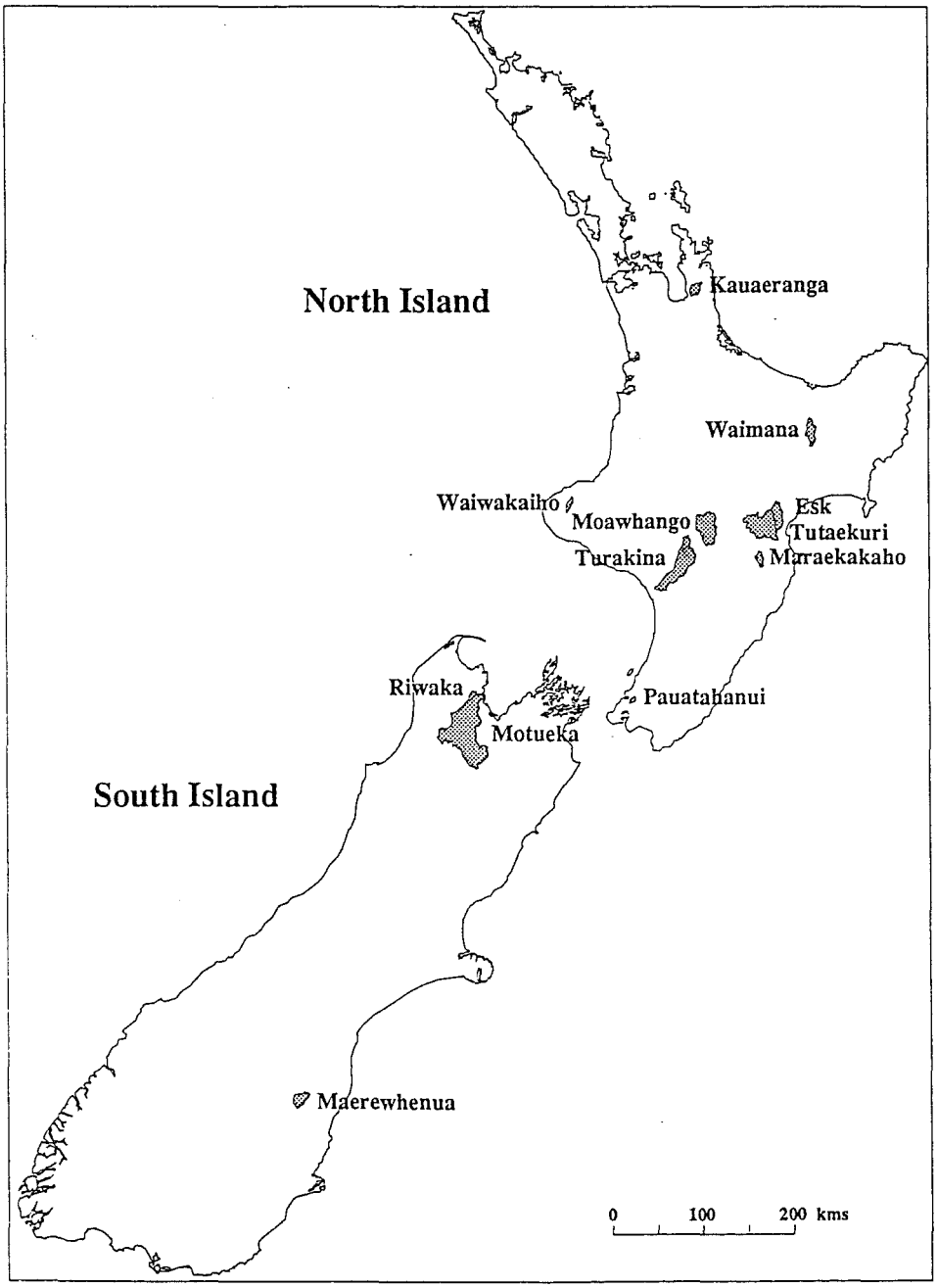


Fig. 2.1. Location of study catchments in New Zealand.

during the study period to enable rating changes to be readily detected. Gaugings generally had a random error of less than 10 %. Bed profile deviations at most of the sites were low. To estimate flows at the three sites with no water level recorders (Motueka River Sites 2, 3 and 5), linear regression equations were developed to equate flows measured on the sampling days with time-paired flow at the nearest upstream recorder site. Because the sites were generally in the same climatic regime the predictive equations were good ($r^2$ = 0.911 - 0.980). The recorder on the Tutaekuri River did not function effectively during low flows, so records there were incomplete. Thus, data from this site had to be dropped from some of the analyses involving flow regime effects.

Each site was visited on a prescribed day every four weeks for 12 months (i.e. 13 samplings per site). The sampling areas were positioned in long (> 50 m) runs which were the most extensive type of habitat in the streams. At each site, one transect was placed across the stream and the width was divided equally into 20 points. Depth and mean velocity (at 0.6 of depth from the surface) were measured at each point using a wading rod and Gurley current meter. Each 4-weekly transect was 1 - 2 m upstream of the previous one to avoid sampling previously disturbed substrata. The transects were located within 1 km of the water level recording stations (except for Motueka Sites 2, 3, and 5).

Periphyton was sampled by collecting a stone located beneath every second point across the transect, resulting in ten replicates per transect. While no conscious bias was used in retrieving stones, this procedure effectively excluded particles less than 50 mm in diameter (too small for the sampling cylinder which was used) and those greater than ca. 400 mm diameter which were too large to lift (these being very rare). The length, width, height dimensions of each sample stone were recorded with the aid of calipers and a rule. Upon retrieval, a 60 mm diameter circle was defined on top of each stone by scribing around a cylinder and all periphytic material (and scrapings of rock) was removed from within it by scraping with a scalpel. The material from each stone was pooled to give a single sample per site, per sampling occasion. Samples were returned to the laboratory on ice.

Duplicate water samples were collected in acid-washed, 500 ml polyethylene bottles on each periphyton sampling day and returned to the laboratory on ice within 24 h. They were frozen until later processing. Field measurements of temperature and conductivity were made using meters. The latter was expressed as mS $m^{-1}$ at 25 $^{o}$C.

When stream flows were too high for full transect sampling (i.e. >1.2 m deep) two half transects, spaced about 5 metres apart, were taken from one bank. On several occasions, flows were too high for any periphyton sampling at some of the Motueka

**Table 2.1** **Summary of disturbance and general hydrological data for the study sites, arranged according to the catchment enrichment groups - see Table 2.2 (1 - average for study period).**

| Group/Site | Median flow ($m^3 s^{-1}$) | Median velocity ($m s^{-1}$) | Flood [1] frequency (no. $y^{-1}$) | Site [1] velocity intensity ($V_{80}$) ($m s^{-1}$) | Flood [1] return int. (d) | Mean stone size (mm-y dim.) |
|---|---|---|---|---|---|---|
| **1: Nutrient rich catchments** | | | | | | |
| Esk | 3.9 | 0.66 | 6 | 0.78 | 55 | 32 |
| Maraekakaho | 0.2 | 0.38 | 2 | 0.44 | 199 | 46 |
| Moawhango | 3.1 | 0.48 | 10 | 0.85 | 31 | 118 |
| Riwaka | 1.4 | 0.44 | 20 | 0.62 | 18 | 120 |
| Turakina | 3.0 | 0.50 | 22 | 0.96 | 15 | 57 |
| Tutaekuri | 11.5 | - | - | - | - | 42 |
| Waiwakaiho | 4.0 | 0.33 | 33 | 0.49 | 11 | 130 |
| **2: Moderately nutrient rich catchments** | | | | | | |
| Kauranga | 2.9 | 0.53 | 23 | 0.86 | 15 | 102 |
| Maerewhenua | 1.7 | 0.54 | 6 | 0.54 | 66 | 60 |
| Motueka-4 | 35.2 | 0.84 | 30 | 1.60 | 7 | 93 |
| Motueka-5 | 43.3 | 0.84 | 29 | 1.18 | 8.6 | 93 |
| Pauatahanui | 0.4 | 0.18 | 12 | 0.33 | 33 | 63 |
| **3: Nutrient poor catchments** | | | | | | |
| Motueka 1 | 4.0 | 0.66 | 31 | 0.91 | 11 | 109 |
| Motueka 2 | 5.3 | 0.54 | 35 | 0.75 | 11 | 104 |
| Motueka 3 | 13.2 | 0.77 | 35 | 1.08 | 9 | 102 |
| Waimana | 5.0 | 0.70 | 19 | 1.10 | 16 | 102 |
| ANOVA | | | | | | |
| F | 1.731 | 1.586 | 4.786 | 1.860 | 1.027 | 0.974 |
| *P* | 0.216 | 0.245 | 0.048 | 0.196 | 0.387 | 0.403 |

River sites. At such times, biomass was nominally defined as zero. Values obtained at these sites soon after floods were generally very low (< 1 mg $m^{-2}$ chlorophyll *a*) whereas at other times they reached greater than 100 mg $m^{-2}$.

*Laboratory procedures*

Each periphyton sample was homogenised in a blender and sub-sampled for analysis within 36 h of collection. For species analysis, aliquots of each sample were settled in an inverted microscope chamber and scanned at 480x and 780x magnification to qualitatively estimate the dominant taxon based on their contribution to the sample's biovolume (i.e. a visual integration of frequency x size). All other taxa were rated on an 8 point scale based on their biovolume in relation to that of the dominant. If two taxa were co-dominant they were both given a score of 8. Generally one, or at most three, taxa made up approximately 70% of the community. Hyrax mounts were prepared for samples containing many small diatoms, or to confirm allocations made under lower power for some more difficult taxa; they were examined under oil immersion at 1250x magnification. Cell counts of individual species were not performed. Non-diatom taxa were identified using Whitford & Schumacher (1973), Bourrelly (1990), and Prescott (1973; 1981); diatoms were identified using Patrick & Reimer (1966; 1975) and Foged (1979). Some of the common filamentous taxa could not be identified to species level because essential distinguishing characteristics were not present (e.g. reproductive structures in *Spirogyra* spp., and *Oedogonium* spp.).

Chlorophyll *a* concentration (corrected for phaeopigments by acidification) was determined spectrophotometrically following hot ethanol extraction (Sartory & Grobbelaar 1984) on 3 replicate 15 - 50 ml aliquots of re-suspended homogenate. Ash-free dry mass was determined after drying at 105 $^{o}$C for 24 h and ashing at 500 $^{o}$C over 4 h. All values for chlorophyll *a* and AFDM are expressed as mass $m^{-2}$ of stream bed in plan view.

Cellular nutrient concentrations ($N_C$ and $P_C$) were estimated on aliquots of homogenised sample (i.e., periphyton plus river water) as total Kjeldahl nitrogen ($H_2SO_4$/Se digestion followed by determination as $NH_4$) and total phosphorus (acid persulphate digestion followed by determination as soluble reactive P), and corrected for background (i.e. river water) nutrient concentrations. Ash-free dry mass was used to standardise values to give $\%N_C$ and $\%P_C$. Since this method does not distinguish between nutrients in healthy algal cells, bacteria, fungi and organic-inorganic detritus there is likely to be some imprecision to all reported values. However, the biovolume of non-algal material was usually low relative to algae at all sites except those in the unenriched catchments.

Water samples were analysed within 1 week of collection. Variables were nitrate-N (automated hydrazine reduction; colorimetry), ammonia-N (automated indophenol

**Table 2.2** **Summary of catchment characteristics of study sites. They are grouped according to an a-priori assessment of potential enrichment (see Methods). All values for Motueka River sites are for % of subcatchment area. (1 = native forest, 2 = high proportion is ungrazed native snow tussock).**

| Group/site | % of Catchment | | | | | | |
|---|---|---|---|---|---|---|---|
| | Geology | | | | Landuse | | |
| | Hard | Soft | Alkaline | Ash | High | Mod. | Forest[1] |
| **1: Nutrient rich catchments** | | | | | | | |
| Esk | 1.1 | 62.7 | 0.8 | 35.4 | 44.6 | 28.3 | 18.4 |
| Maraekakaho | 59.5 | 41.0 | 0.9 | 0.0 | 84.0 | 12.0 | 0.0 |
| Moawhango | 3.0 | 9.5 | 0.0 | 87.6 | 11.8 | 62.4 | 9.7 |
| Riwaka | 40.2 | 0.0 | 47.4 | 0.0 | 0.9 | 11.1 | 32.6 |
| Turakina | 9.5 | 81.7 | 0.0 | 4.9 | 17.9 | 77.0 | 1.7 |
| Tutaekuri | 4.9 | 48.9 | 0.3 | 37.4 | 46.8 | 19.0 | 9.3 |
| Waiwakaiho | 28.5 | 0.0 | 0.0 | 71.6 | 38.1 | 6.4 | 46.2 |
| **2: Moderately nutrient rich catchments** | | | | | | | |
| Kauranga | 76.2 | 0.0 | 0.0 | 23.8 | 4.5 | 2.2 | 74.6 |
| Maerewhenua | 96.7 | 0.0 | 0.0 | 0.0 | 1.7 | 98.3[2] | 0.0 |
| Motueka-4 | 83.6 | 9.9 | 6.5 | 0.0 | 10.9 | 24.1 | 42.6 |
| Motueka-5 | 88.6 | 0.0 | 11.4 | 0.0 | 11.2 | 7.3 | 37.1 |
| Pauatahanui | 100.0 | 0.0 | 0.0 | 0.0 | 22.3 | 66.8 | 6.6 |
| **3: Nutrient poor catchments** | | | | | | | |
| Motueka 1 | 100 | 0.0 | 0.0 | 0.0 | 0.0 | 48.3[2] | 48.4 |
| Motueka 2 | 100 | 0.0 | 0.0 | 0.0 | 0.5 | 66.1[2] | 25.5 |
| Motueka 3 | 100 | 0.0 | 0.0 | 0.0 | 13.9 | 41.5 | 22.9 |
| Waimana | 80.0 | 0.3 | 0.0 | 20.0 | 0.0 | 3.0 | 97.0 |

blue), and soluble reactive phosphorus (automated molybdate with ascorbic acid reduction). See Biggs (1990; table 2) for further details.

*Data analysis*

Difficulties arise in defining a biologically significant measure of flow variability and disturbance in studies of temperate streams where many minor freshets occur across a range of bed gradients. Several arbitrary approaches have been adopted in the past, three of which are to compare the magnitude of change in flow with that on the preceding 5 days (Biggs & Close, 1989), or the baseflow (Grimm & Fisher, 1989; Feminella & Resh, 1990), or the flow required to initiate bed movement (McElravy *et al.*, 1989; Poff, 1992). Periphyton scouring by floods is fundamentally linked with increases in water velocity (plucking/tearing of cells at moderate velocities, and abrasion by sediment movement at high velocities). Therefore, I considered that a measure of the changes in water velocity over time would be the most appropriate descriptor of disturbance regimes. Hydraulic geometry equations (Mosley 1983) were calibrated for each sampling reach using the hydraulic data collected on the 4-weekly visits (Fig. 2.2).

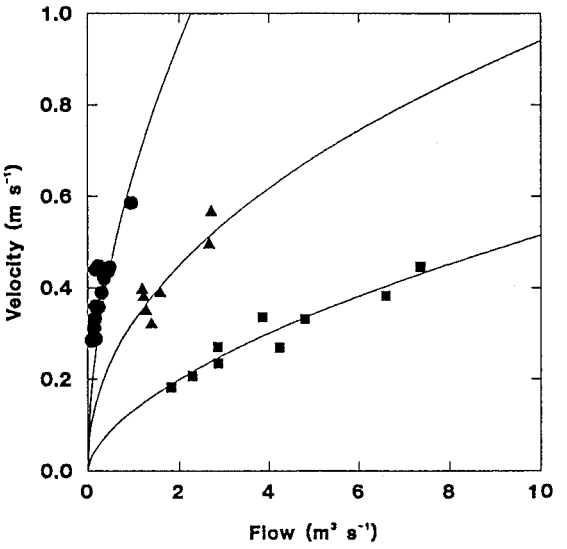


Fig. 2.2. Mean transect velocity as a function of discharge at three sites (■, Waiwakaiho River; ●, Turakina River; ▲, Maraekakaho River).

These equations were then used to convert flow records to continuous velocity records for the study period (Fig. 2.3). It should be noted that because some of the streams could not be waded during high flows, the upper velocities for floods are estimates based on extrapolations from the models. Previous experience for similar, confined channels in locations where gauging has been possible during floods has shown that these models generally represent flow-velocity relationships accurately up to bankfull discharges (e.g. Biggs 1982; fig. 4). A disturbance was defined as any flow event where mean cross-section velocity exceeded 1 m $s^{-1}$, since approximately 90% of the

area of streambeds (in a sample of 65 reaches) in New Zealand have velocities < 1 m $s^{-1}$ during median flows (Biggs *et al.*, 1990).

The following disturbance parameters were developed:

a) number of floods per year- the frequency of events when the hydrograph rose to over 1 m $s^{-1}$;

b) velocity intensity ($V_{80}$)- the 80th percentile mean cross-section velocity (calculated using velocity duration curves). This incorporates flood peaks and their recessions, and is interpreted to be a measure of the overall intensity of physical disturbance at a site;

c) flood return interval - the mean time between floods (days per year where V < 1 m $s^{-1}$ divided by the number of events per year where V > 1 m $s^{-1}$).

Velocity duration curves were also used to determine median velocities over the study period.

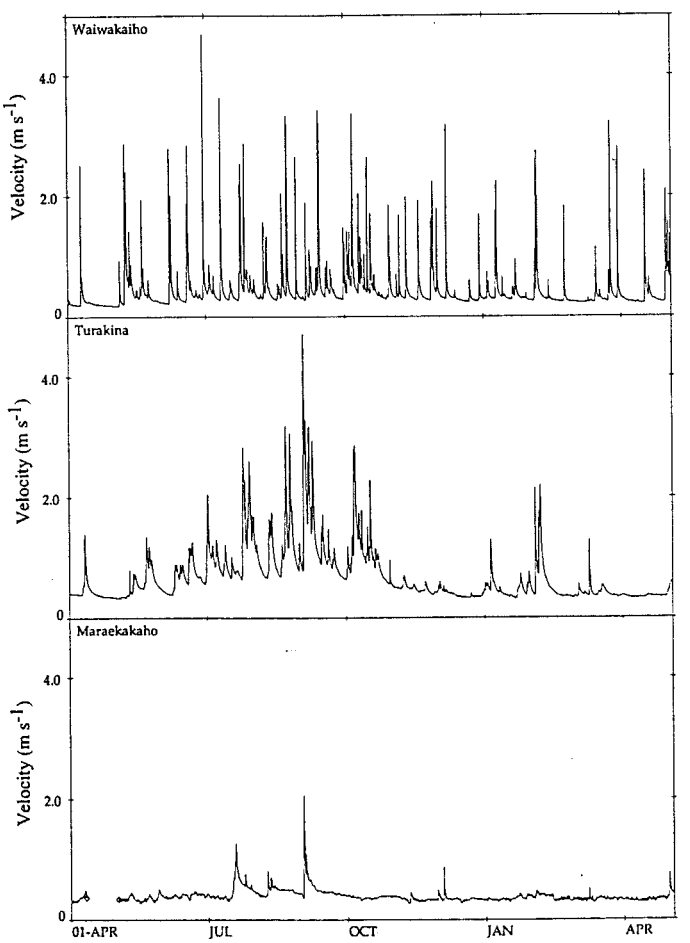


Fig. 2.3. Velocity - time plots for three of the study rivers with high, medium, and low frequency floods. Sites as for Fig. 2.2.

Data for most variables were log transformed and geometric means calculated for the full year (described as mean monthly values in the text) because the 13 data points for each site were generally log-normally distributed. The degree of variability within the data was determined as the percentage coefficient of variation (% C.V.).

Quantitative differences in variables among catchment groups were assessed with one-way ANOVA. The relative contribution of disturbance and catchment characteristics to variance in mean monthly chlorophyll *a* concentrations among the 16 sites was determined using step-wise multiple regression and co-variance procedures. Models were fitted to non-linear relationships using non-linear fitting procedures. All analyses were carried out with SYSTAT (Wilkinson, 1990).

## III. Results

*Flow regimes*

Median stream flow varied widely among the study sites: from 0.2 $m^3 s^{-1}$ to 43.3 $m^3 s^{-1}$ (Table 2.1). Median stream velocities over the study period ranged from 0.18 m $s^{-1}$ to 0.84 m $s^{-1}$, with those at most sites being > 0.4 m $s^{-1}$. Flood frequency for the study period also varied widely (2 - 35 per year), and site velocity intensities ranged from 0.33 m $s^{-1}$ to 1.60 m $s^{-1}$. Flood return periods varied from 7 days to 199 days (Table 2.1). This latter statistic also indicates the average number of days potentially available for periphyton accrual at each site. Velocity - time plots for several sites demonstrate the range in frequency and time intervals between floods over the study period (Fig. 2.3). A slightly higher number of events, and thus higher average flows, occurred in winter and spring at some sites (e.g. Turakina River, Fig. 2.3).

Only flood frequency differed significantly ($P$ <0.05) among catchment enrichment groups (Table 2.1). All other flow, disturbance and substrate size parameters varied widely within the groups.

*Nutrient regimes of catchment groups*

Mean monthly water temperatures at the sites were generally in the 8 - 16 $^oC$ range, but dissolved inorganic nutrients and conductivity varied greatly among sites (Table 2.3). Variability within sites was low for conductivity (mean %C.V.= 9.8), and moderate for dissolved reactive P and total inorganic N (mean %C.V.= 18.0 for both nutrients). Conductivity, and concentrations of bicarbonate and silica, differed significantly (i.e. $P < 0.05$) between the three catchment enrichment groups (Table 2.3). The nutrient rich group averaged 27.1 mS $m^{-1}$ conductivity, 131 mg $l^{-1}$ bicarbonate, and 16.4 mg $l^{-1}$ silica; the moderately nutrient rich group averaged 10.6 mS $m^{-1}$, 37 mg $l^{-1}$, and 9.0 mg $l^{-1}$; and the nutrient poor group averaged 8.7 mS $m^{-1}$,

**Table 2.3** **Summary of geometric mean (and coefficient of variation) water quality results from the study sites (n = 13 for all sites) arranged according to catchment enrichment groups (see Table 2) (TSS = total suspended solids, DRP = dissolved reactive-P, TIN = total inorganic N).**

| Group/Site | Temperature (°C) | Conductivity (mS $m^{-1}$) | TSS (mg $l^{-1}$) | Bicarb. (mg $l^{-1}$) | Silica (mg $l^{-1}$) | DRP ($\mu$g $l^{-1}$) | TIN ($\mu$g $l^{-1}$) |
|---|---|---|---|---|---|---|---|
| **1: Nutrient rich catchments** | | | | | | | |
| Esk $\bar{x}$ | 12.6 | 28.3 | 5.7 | 151 | 14.7 | 7.7 | 82 |
| %C.V. | 11.9 | 7.7 | 50.5 | 4.2 | 5.3 | 23.3 | 31.5 |
| Maraekakaho $\bar{x}$ | 15.0 | 45.5 | 1.0 | 211 | 21.0 | 21.2 | 78 |
| % C.V. | 10.2 | 7.3 | 114.7 | 5.5 | 3.6 | 15.2 | 31.0 |
| Moawhango $\bar{x}$ | 10.8 | 13.5 | 3.7 | 59 | 21.8 | 4.1 | 80 |
| % C.V. | 16.1 | 5.9 | 59.1 | 7.4 | 5.9 | 22.8 | 15.7 |
| Riwaka $\bar{x}$ | 10.8 | 15.8 | 1.4 | 96 | 7.9 | 5.7 | 172 |
| % C.V. | 5.9 | 8.8 | 63.4 | 5.8 | 9.4 | 15.6 | 8.0 |
| Turakina $\bar{x}$ | 14.8 | 32.0 | 19.5 | 135 | 15.1 | 25.3 | 224 |
| % C.V. | 11.1 | 12.3 | 69.2 | 9.6 | 5.5 | 12.3 | 21.0 |
| Tutaekuri $\bar{x}$ | 16.3 | 27.6 | 5.6 | 132 | 13.1 | 6.2 | 64 |
| % C.V. | 10.4 | 5.3 | 47.4 | 3.6 | 5.0 | 30.9 | 34.0 |
| Waiwakaiho $\bar{x}$ | 12.4 | 12.0 | 1.3 | 46 | 21.4 | 20.1 | 133 |
| % C.V. | 7.0 | 12.4 | 73.3 | 13.6 | 11.8 | 16.2 | 17.0 |
| **2: Moderately nutrient rich catchments** | | | | | | | |
| Kauranga $\bar{x}$ | 15.5 | 7.9 | 1.2 | 13 | 11.2 | 1.8 | 55 |
| % C.V. | 7.5 | 17.5 | 77.8 | 10.2 | 28.6 | 28.9 | 18.7 |
| Maerewhenua $\bar{x}$ | 9.8 | 6.6 | 0.5 | 33 | 7.1 | 3.6 | 26 |
| % C.V. | 25.5 | 8.9 | 65.8 | 4.4 | 13.3 | 22.4 | 19.9 |
| Motueka 4 $\bar{x}$ | 12.4 | 9.9 | 2.5 | 47 | 8.0 | 5.7 | 162 |
| % C.V. | 13.4 | 9.0 | 74.6 | 5.1 | 10.4 | 10.3 | 9.8 |
| Motueka 5 $\bar{x}$ | 12.6 | 11.3 | 2.4 | 55 | 8.2 | 4.2 | 113 |
| % C.V. | 11.9 | 7.9 | 70.5 | 4.9 | 7.9 | 20.4 | 11.2 |
| Pauhatahanui $\bar{x}$ | 13.2 | 15.6 | 4.0 | 30 | 11.5 | 28.7 | 232 |
| % C.V. | 9.8 | 2.3 | 30.5 | 5.5 | 18.7 | 10.9 | 17.1 |
| **3. Nutrient poor catchments** | | | | | | | |
| Motueka 1 $\bar{x}$ | 8.4 | 9.2 | 0.4 | 51 | 9.1 | 3.8 | 35 |
| % C.V. | 14.7 | 6.5 | 100.8 | 2.6 | 9.8 | 11.1 | 8.5 |
| Motueka 2 $\bar{x}$ | 12.1 | 9.8 | 1.1 | 53 | 9.7 | 3.0 | 28 |
| % C.V. | 12.5 | 6.3 | 88.2 | 3.7 | 9.5 | 19.5 | 14.2 |
| Motueka 3 $\bar{x}$ | 13.4 | 7.8 | 0.9 | 39 | 10.0 | 3.7 | 170 |
| % C.V. | 12.6 | 8.5 | 90.0 | 6.1 | 12.3 | 21.1 | 10.6 |
| Waimana $\bar{x}$ | 12.6 | 7.9 | 1.6 | 32 | 17.1 | 17.1 | 52 |
| % C.V. | 8.7 | 29.7 | 109 | 5.2 | 12.5 | 6.7 | 21.6 |
| ANOVA | | | | | | | |
| F | 0.732 | 6.607 | 1.506 | 7.822 | 4.798 | 0.607 | 0.697 |
| *P* | 0.500 | 0.010 | 0.258 | 0.006 | 0.028 | 0.560 | 0.516 |

**Table 2.4** **Correlation coefficients for pairwise comparisons of the disturbance, catchment, water quality and periphyton chlorophyll *a* data among the sites (N = 15 or 16) (* $P<0.05$, ** = $P<0.01$, *** = $P<0.001$).**

| Variable | Flood frequency | Velocity intensity | Hard rocks | Soft rocks | Alkaline rocks | Ash rocks | High landuse | Mod. landuse | Forest |
|---|---|---|---|---|---|---|---|---|---|
| Vel. intensity | 0.485 | | | | | | | | |
| Hard rocks | 0.359 | 0.134 | | | | | | | |
| Soft rocks | -0.389 | -0.010 | -0.649** | | | | | | |
| Alk. rocks | 0.042 | -0.027 | -0.123 | -0.169 | | | | | |
| Ash rocks | -0.132 | -0.140 | -0.661** | 0.013 | -0.218 | | | | |
| High landuse | -0.471 | -0.397 | -0.366 | 0.515* | -0.208 | 0.142 | | | |
| Mod. landuse | -0.189 | -0.220 | -0.083 | 0.157 | -0.312 | -0.129 | -0.245 | | |
| Forest | 0.435 | 0.417 | 0.232 | -0.435 | 0.039 | 0.092 | -0.406 | -0.657** | |
| Temperature | -0.071 | 0.013 | -0.145 | 0.416 | -0.220 | -0.066 | 0.464 | -0.328 | 0.017 |
| Conductivity | -0.548* | -0.323 | -0.513 | 0.806*** | -0.019 | -0.054 | 0.830*** | -0.051 | -0.515* |
| TSS | -0.100 | 0.106 | -0.537* | 0.803*** | -0.116 | 0.005 | 0.078 | 0.344 | -0.344 |
| Bicarbonate | -0.498 | -0.237 | -0.534* | 0.784*** | 0.116 | -0.075 | 0.770*** | -0.089 | -0.492 |
| Silica | -0.344 | -0.303 | -0.631* | 0.341 | -0.348 | 0.726** | 0.608* | -0.202 | -0.048 |
| DRP | -0.277 | -0.410 | -0.221 | 0.407 | -0.197 | 0.015 | 0.501 | 0.034 | -0.204 |
| TIN | 0.117 | 0.031 | -0.194 | 0.258 | 0.276 | -0.138 | 0.115 | 0.039 | -0.302 |
| Chl. *a* | -0.561* | -0.434 | -0.212 | 0.316 | 0.243 | -0.129 | 0.771*** | -0.277 | -0.349 |
| Ln chl. *a* | -0.712** | -0.535* | -0.526* | 0.397 | 0.375 | 0.134 | 0.663** | 0.161 | -0.484 |

44 mg $l^{-1}$ and 11.4 mg $l^{-1}$. No significant differences were recorded for dissolved inorganic nutrients (DRP and TIN) between enrichment groups.

Few significant linear correlations occurred between flood/catchment/water quality regimes (Table 2.4), but conductivity was negatively correlated with flood frequency. The strongest correlations were for the proportion of catchments in soft rocks vs. conductivity, total suspended solids and bicarbonate (Table 2.4). Silica concentration was correlated strongly with the proportion of ash rocks in the catchment, and high intensity landuse, but no significant differences in dissolved N and P concentrations were associated with landuse. Lastly, no significant correlations ($P > 0.05$) were found between either dissolved, or cellular, nutrient concentrations and disturbance frequency of the sites (data in Tables 2.1, 2.3, and 2.5).

Although considerable variation in cellular nutrient concentration was found within sites (geometric mean %C.V. = 175 for $P_c$ and 44 for $N_c$), periphyton appeared to be more N than P deficient for growth because cellular P concentrations were usually > 0.5% (Auer & Canale, 1982) and the $N_c$:$P_c$ ratios were below 10. Periphyton from nutrient-rich catchments had considerably higher average cellular N concentrations than periphyton from the other sites (Fig. 2.4), and the among-catchment group ANOVA was highly significant ($P << 0.001$; Table 2.5). In contrast, little difference in mean monthly cellular P concentrations occurred between enrichment groups (Fig.2.4, Table 2.5), and neither mean cellular P nor N correlated significantly with DRP and TIN ($P > 0.05$).

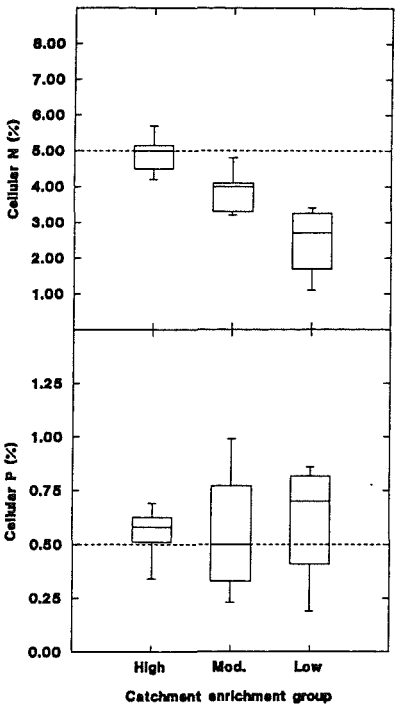


Fig. 2.4. Box plots of cellular nutrient concentration for the three catchment enrichment groups. The central line in each box denotes the median, the upper and lower edges are the interquartile ranges, and the error bars are 1.5 times the interquartile range (see Wilkinson 1990). The dashed line denotes the 0.5% $P_C$ and 5% $N_C$ values below which nutrient deficiency is expected to occur.

When the sites were plotted individually (Fig. 2.5a), a significant negative correlation ($P$ = 0.024) was found between mean monthly cellular nitrogen concentrations and proportion of the catchments in (nutrient poor) hard rocks. A highly significant curvilinear relationship ($P$ < 0.001) occurred between cellular N concentrations and proportion of the catchments developed for intensive agriculture (Fig. 2.5b). One site was an outlier to this relationship (Riwaka River), and the high cellular N observed there could be attributed to the alkaline rock type of the catchment rather than landuse (Biggs & Gerbeaux, 1993). These relationships suggest that the sites could be placed on a nutrient resource gradient even though this was not shown by the stream nutrient data. Because dissolved nutrient concentrations can be heavily influenced by instream processes such as uptake by microbial communities (e.g. Mulholland & Rosemond, 1992), they need not reflect overall loadings to the streams (see Discussion).

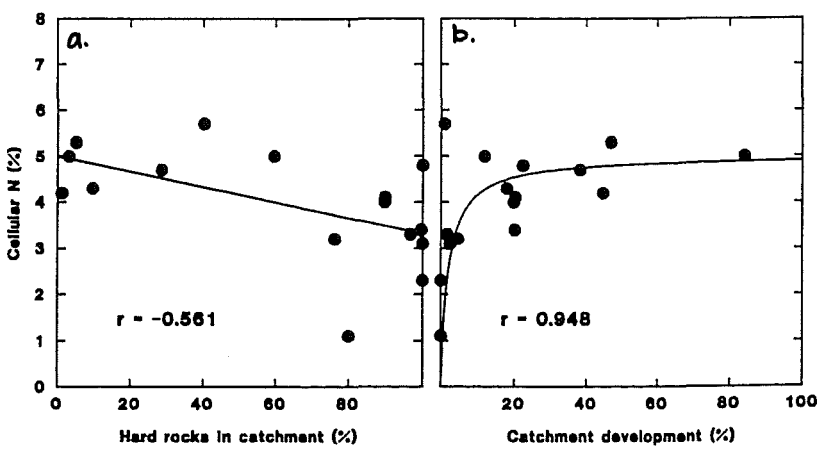


Fig. 2.5. Mean monthly cellular nitrogen (%$N_C$) as a function of the proportion of the catchment in hard rocks (a) and intensive agricultural development (b).

*Periphyton responses*

Average community compostion (by biovolume) was generally dominated by diatoms (Table 2.5), with *Gomphoneis herculeana*, *Synedra ulna*, or *Cymbella kappii* abundant at many of the sites. Thus, no clear differences in average community composition were evident among the enrichment groups. However, the structure of the communities changed appreciably during periods of low-flow. At these times communities in the nutrient rich catchments were more commonly dominated by filamentous taxa (e.g. *Cladophora glomerata*; Table 2.6) and in the nutrient poor catchments they were dominated by diatoms (e.g. *Gomphoneis herculeana* and *Synedra ulna*).

Chlorophyll *a* maxima occurred in winter and summer (May/June/July and December/January/February) at sites where floods had a low frequency (e.g. Maraekakaho River; Fig. 2.6). Seasonality was often masked by sloughing at sites with a medium frequency of floods, and chlorophyll *a* peaks occurred when low flows presented opportunities for accrual. At sites with high frequency floods, chlorophyll *a* concentration was generally low and displayed few peaks (e.g. Waiwakaiho River; Fig. 2.6). Some variations within these three regimes occurred. Most notable was for several sites characterised by frequent floods where moderate biomass peaks occurred in late summer during an unusually long low-flow period. Chlorophyll *a* concentration at these sites exceeded 100 mg $m^{-2}$ at that time (data not shown).

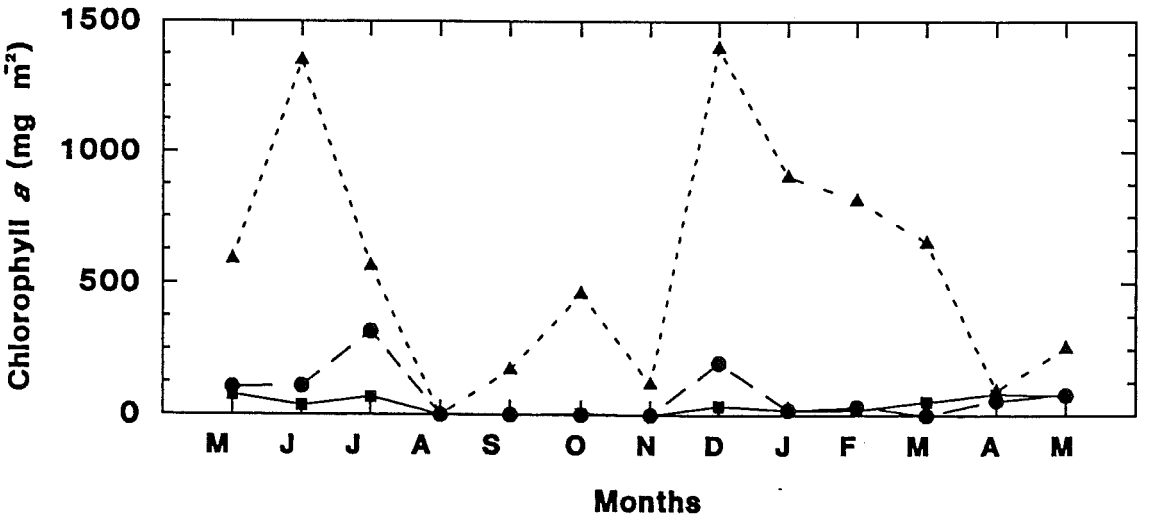


Fig. 2.6. Temporal fluctuations in chlorophyll *a* concentration for the Waiwakaiho (■), Turakina (●), and Maraekakaho (▲) Rivers (Fig. 2.3 for temporal velocity regimes).

**Table 2.5** **Summary of geometric mean (and co-efficient of variation) periphyton results from the sampling sites arranged according to the catchment enrichment groups (see Table 2.2).**

| Group/Site | Chlorophyll (mg $m^{-2}$) | AFDM (g $m^{-2}$) | $P_c$ (%) | $N_c$ (%) | Dominant taxa |
|---|---|---|---|---|---|
| 1: Nutrient rich catchments | | | | | |
| Esk $\bar{x}$ | 54.5 | 16.3 | 0.49 | 4.2 | *Synedra ulna, Navicula avenacea* |
| % C.V. | 48.3 | 61.0 | 164.6 | 35.6 | *Fragilaria vaucheriae* |
| Maraekakaho $\bar{x}$ | 280.8 | 69.5 | 0.69 | 5.0 | *Cladophora glomerata, Cocconeis* sp. |
| % C.V. | 33.7 | 45.9 | 304.9 | 45.2 | *Fragilaria vaucheriae* |
| Moawhango $\bar{x}$ | 25.5 | 22.1 | 0.34 | 5.0 | *Cymbella kappii; S. ulna, Cocconeis* |
| % C.V. | 72.7 | 24.2 | 97.3 | 12.3 | sp. |
| Riwaka $\bar{x}$ | 109.4 | 17.1 | 0.66 | 5.7 | *Cymbella kappii, Melosira varians,* |
| % C.V. | 21.5 | 27.5 | 274.8 | 18.4 | *Cymbella minuta* |
| Turakina $\bar{x}$ | 14.2 | 4.6 | 0.58 | 4.3 | *Cocconeis* sp., *Cladophora glomerata,* |
| % C.V. | 86.1 | 27.6 | 114.3 | 23.4 | *Rhoicosphenia curvata* |
| Tutaekuri $\bar{x}$ | 41.4 | 15.4 | 0.53 | 5.3 | *Gomphoneis herculeana, Cymbella kappii,* |
| % C.V. | 61.7 | 51.6 | 113.8 | 22.1 | *Synedra ulna* |
| Waiwakaiho $\bar{x}$ | 15.2 | 8.9 | 0.59 | 4.7 | *Melosira varians, Navicula avenacea,* |
| % C.V. | 62.9 | 36.6 | 166.1 | 41.7 | *Gomphoneis herculeana* |
| 2: Moderately nutrient rich catchments | | | | | |
| Kauranga $\bar{x}$ | 17.0 | 5.9 | 0.23 | 3.2 | *Cymbella kappii, Synedra ulna,* |
| % C.V. | 61.4 | 48.6 | 53.0 | 30.3 | *Achnanthes minutissima* |
| Maerewhenua $\bar{x}$ | 17.0 | 6.4 | 0.33 | 3.3 | *Gomphoneis herculeana, Synedra ulna,* |
| % C.V. | 51.5 | 58.6 | 94.6 | 46.1 | *Cymbella kappii* |
| Motueka 4 $\bar{x}$ | 7.0 | 5.5 | 0.50 | 4.0 | *Gomphoneis herculeana, Synedra ulna,* |
| % C.V. | 102.0 | 58.8 | 112.7 | 30.7 | *Cymbella kappii* |
| Motueka 5 $\bar{x}$ | 9.5 | 5.5 | 0.77 | 4.1 | *Synedra ulna, Gomphoneis herculeana,* |
| % C.V. | 75.3 | 54.0 | 334.7 | 38.1 | *Cymbella kappii* |
| Pauatahanui $\bar{x}$ | 22.9 | 7.5 | 0.99 | 4.8 | *Melosira varians, Navicula avenacea,* |
| % C.V. | 39.1 | 33.2 | 5482.3 | 15.9 | *Rhoicosphenia curvata* |
| 3: Nutrient poor catchments | | | | | |
| Motueka 1 $\bar{x}$ | 2.2 | 1.9 | 0.86 | 2.3 | *Gomphoneis herculeana, Synedra ulna,* |
| % C.V. | 103.8 | 46.9 | 94.6 | 125.3 | *Cymbella kappii* |
| Motueka 2 $\bar{x}$ | 2.4 | 1.9 | 0.77 | 3.1 | *Synedra ulna, Cymbella kappii,* |
| % C.V. | 93.7 | 63.8 | 268.6 | 86.4 | *Gomphoneis elegans* |
| Motueka 3 $\bar{x}$ | 2.9 | 1.8 | 0.63 | 3.4 | *Synedra rumpens, Navicula avenacea,* |
| % C.V. | 98.6 | 60.3 | 169.8 | 61.5 | *Gomphonema parvulum* |
| Waimana $\bar{x}$ | 2.1 | 1.8 | 0.19 | 1.1 | *Gomphoneis herculeana, Synedra ulna* |
| % C.V. | 89.4 | 68.9 | 105.8 | 1685 | *Fragilaria vaucheriae* |
| ANOVA | | | | | |
| F | 2.198 | 2.938 | 0.080 | 14.661 | |
| *P* | 0.151 | 0.089 | 0.924 | 0.001 | |

Mean monthly chlorophyll *a* varied from as little as 2.1 mg $m^{-2}$ in the Waimana River (unenriched catchment group) to 280.8 mg $m^{-2}$ in the Maraekakaho Stream (nutrient rich catchment group) (Table 2.5). AFDM ranged from 1.8 g $m^{-2}$ to 69.5 g $m^{-2}$ at these sites. Temporal variability in chlorophyll *a* and AFDM at individual sites was high (average %C.V. = 69 and 48, respectively), and mean annual values for sites within the enrichment groups also varied widely. With such high variability, the between catchment group ANOVAs were not significant at $P = 0.05$ for chlorophyll *a* and AFDM.

Mean monthly chlorophyll *a* concentration was negatively correlated with flood frequency (Table 2.4). It decreased from approximately 80 mg $m^{-2}$ where flood frequency was less than 5 $yr^{-1}$ to approximately 8 mg $m^{-2}$ where it was greater than 30 $yr^{-1}$ (Fig. 2.7) . Thus, the shorter the return interval of floods, the less periphyton that was present. Chlorophyll *a* concentration was also correlated negatively with the proportion of the catchment in nutrient poor hard rocks and forest (Table 2.4). However, it was significantly and positively correlated with degree of landuse.

**Table 2.6 Highest low flow chlorophyll *a*, and taxa dominating at the time, for the study sites.**

| Site | Chlorophyll *a* (mg $m^{-2}$) | Dominant taxa |
|---|---|---|
| **1: Nutrient rich catchments** | | |
| Esk | 769 | *Vaucheria* sp., *Epithemia sorex, Synedra ulna* |
| Maraekakaho | 1396 | *Vaucheria* sp., *Synedra ulna, Cladophora glomerata* |
| Moawhango | 402 | *Synedra ulna, Gomphoneis herculeana* |
| Riwaka | 566 | *Cymbella kappii, Cymbella minuta* |
| Turakina | 317 | *Cladophora glomerata, Rhoicosphenia curvata* |
| Tutaekuri | 802 | *Cladophora glomerata, Epithemia sorex* |
| Waiwakaiho | 82 | *Melosira varians* |
| **2: Moderately nutrient rich catchments** | | |
| Kauranga | 163 | *Spirogyra* sp. |
| Maerewhenua | 108 | *Gomphoneis herculeana, Synedra ulna* |
| Motueka 4 | 351 | *Gomphoneis herculeana, Synedra ulna* |
| Motueka 5 | 126 | *Synedra ulna, Stigeoclonium* sp. |
| Pauatahanui | 163 | *Nitzschia linearis, Navicula avenacea* |
| **3: Nutrient poor catchments** | | |
| Motueka 1 | 48 | *Gomphonema tenellum, Synedra ulna* |
| Motueka 2 | 48 | *Gomphoneis herculeana, Synedra ulna* |
| Motueka 3 | 173 | *Synedra* sp., *Gomphonema tenellum* |
| Waimana | 123 | *Gomphoneis herculeana* |
| ANOVA | | |
| F | 5.438 | |
| *P* | 0.019 | |

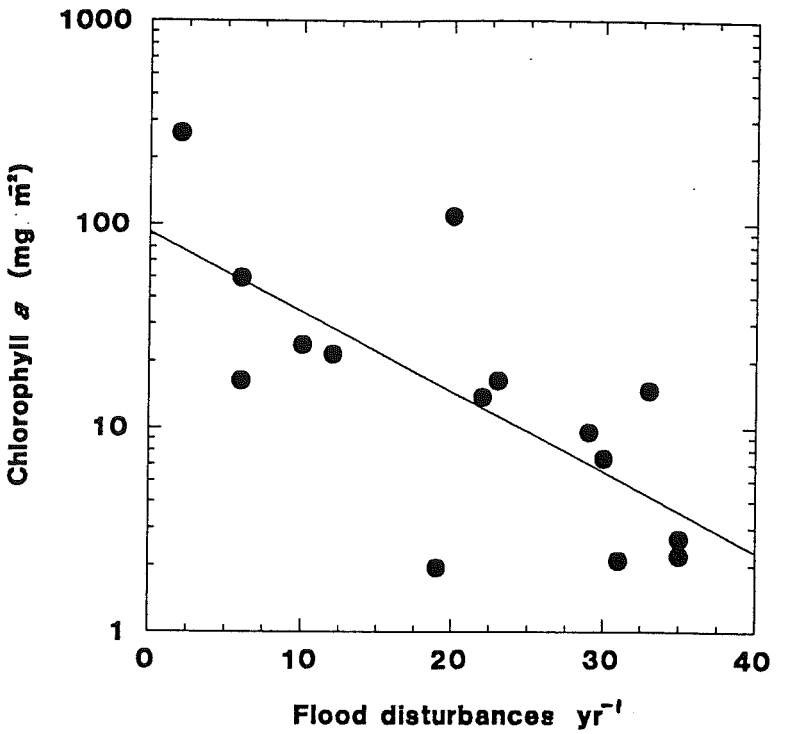


Fig. 2.7. Mean monthly chlorophyll *a* as a function of flood disturbance frequency (see Table 2.4 for correlation statistics). One site is omitted because of an insufficient hydrological record during the study period (see Methods).

*Combined flood disturbance - nutrient enrichment effects*

Mean monthly chlorophyll *a* concentrations are plotted as a function of site velocity intensities in Fig. 2.8. Sites are identified by symbols according to their catchment enrichment groups. Separate relationships between biomass and velocity intensity ($V_{80}$) occurred for the different enrichment groups. Only one site (the Waiwakaiho River) did not regress with the rest of the members of its group. Increasing velocity

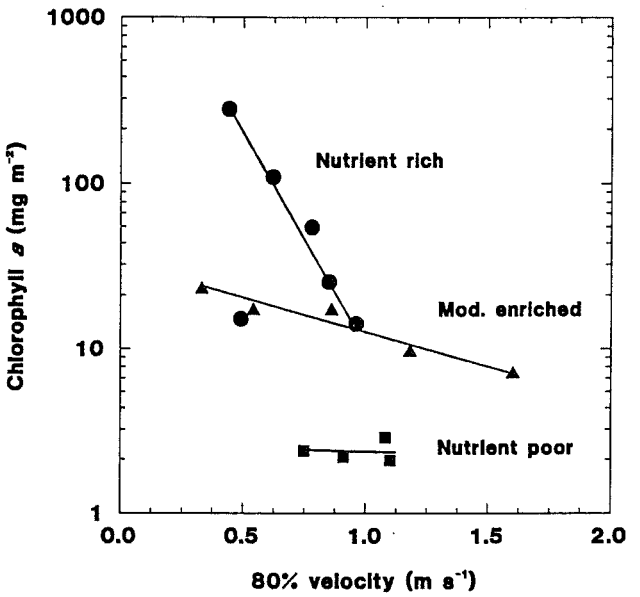


Fig. 2.8. Mean monthly chlorophyll *a* concentrations as a function of the 80% velocity duration at each site. The three distinct relationships are labelled according to the catchment enrichment group (Table 2.2) they represent. One site is omitted because of an insufficient hydrological record during the study period (see Methods).

intensity had a strong negative effect on mean monthly chlorophyll *a* concentration at sites from the high and moderate enrichment groups. Further, chlorophyll *a* biomass was progressively higher under high than moderate enrichment for a given velocity intensity when values of $V_{80}$ were < 0.80 m $s^{-1}$. The group of low enrichment sites appeared to be under such high nutrient stress (Fig. 2.4) that too little growth occurred during interflood periods for flood disturbance to be an important controller of accrual.

Regression analysis of these relationships was performed with the Waiwakaiho River re-classified to the moderate enrichment group (the only site with a highly developed catchment that had significant riparian vegetation along the channel which could have ameliorated the effects of enrichment from agriculture). The high and moderate enrichment groups had highly significant slopes for the chlorophyll *a* - $V_{80}$ relationships, but the low enrichment group did not (Table 2.7). Overall, slopes of the three relationships were significantly different (F ratio = 66.218, $P < 0.001$ for the enrichment group x velocity interaction). However, most of this difference was due to the high and moderate enrichment groups. When the moderate and low enrichment groups were compared, the slopes for these two were not different (F ratio = 2.486, $P = 0.166$). Thus, it appears that at moderate to high levels of nutrient enrichment, flood disturbance has a primary role in structuring patterns of inter-catchment development of periphyton. However, under low enrichment, the flood disturbance regime may become a less important controller of biomass.

**Table 2.7** **Regression analysis of $\log_e$ chlorophyll *a* as a function of velocity intensity ($V_{80}$) for the three catchment enrichment groups. The Waiwakaiho River was re-classified into the moderate enrichment group for this analysis.**

| Predictors | Coefficient | Std Error | T value | P(2 tail) |
|---|---|---|---|---|
| 1: High enrichment N=5 | $R^2$ = 0.985 | | | |
| Constant | 8.234 | 0.306 | 26.943 | 0.000 |
| $V_{80}$ | -5.738 | 0.406 | -14.129 | 0.001 |
| | - | | | |
| 2: Moderate enrichment N=6 | $R^2$ = 0.889 | | | |
| Constant | 3.329 | 0.142 | 23.407 | 0.000 |
| $V_{80}$ | -0.852 | 0.151 | -5.648 | 0.005 |
| 3: Low enrichment N=4 | $R^2$ = 0.014 | | | |
| Constant | 0.768 | 0.593 | 1.296 | 0.324 |
| $V_{80}$ | 0.104 | 0.611 | 0.170 | 0.881 |

The relative contributions of flood frequency and intensity, and catchment nutrient regimes, to the primary habitat template of the periphyton was assessed using multiple regression (data in Tables 1, 2, and 5). Three variables were chosen during stepwise discrimination as the best predictors of chlorophyll *a* concentration: flood frequency, proportion of the catchment in intensive landuse, and proportion of alkaline rocks in the catchment (Table 2.8). These three variables could not be ranked clearly for explanatory power and jointly they explained 89% of the variance in mean monthly chlorophyll *a* among the sites.

**Table 2.8** **Multiple regression coefficients and statistics for $\log_e$ chlorophyll *a* as a function of disturbance frequency and catchment characteristics (N = 15, $R^2$ = 0.890).**

| Predictors | Coefficient | Std Error | T value | *P* (2 Tail) |
|---|---|---|---|---|
| Constant | 3.026 | 0.412 | 7.352 | 0.001 |
| Disturbance freq. | -0.060 | 0.014 | -4.207 | 0.001 |
| High landuse | 0.034 | 0.007 | 4.692 | 0.001 |
| Alkaline rocks | 0.059 | 0.012 | 4.972 | 0.001 |

Finally, the development of periphyton as a function of both flood disturbance and enrichment is depicted in Fig. 2.9. The effects of geology and landuse are combined onto one enrichment axis using cellular-N concentrations. This variable is closely related to catchment conditions (see Fig. 2.4 and 2.5) and also is a direct measure of the nutrient status of the periphyton. The plot provides both a summary of the empirical results of this study and a theoretical basis for understanding the relative (and interactive) influences of disturbance and enrichment as fundamental axes of the habitat template of stream periphyton. It shows that a combination of infrequent flood disturbances and high levels of enrichment are necessary to attain a high average biomass of periphyton. Conversely, if flood disturbances are very frequent, and/or levels of enrichment are very low, there will be only a very low average biomass of periphyton. High levels of enrichment (e.g. > 4% $N_C$) can result in some periphyton accrual at high frequencies of flood disturbance (e.g. > 20 events $yr^{-1}$), presumably because of more rapid inter-flood regeneration, and some periphyton can also develop with low levels of enrichment (e.g. < 2% $N_C$) providing flood frequency is also low (e.g. < 10 events $yr^{-1}$).

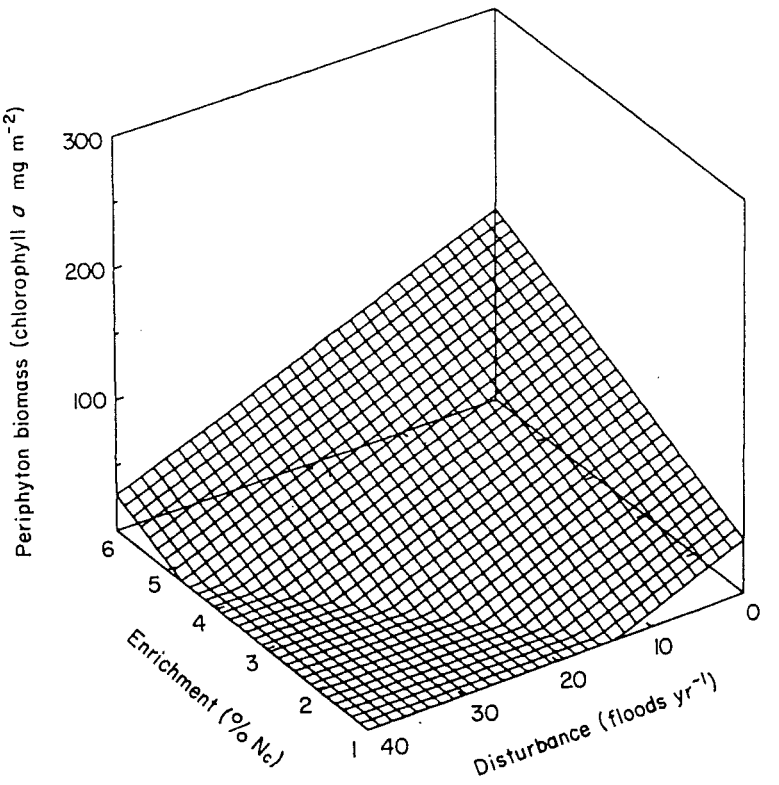


Fig. 2.9. Three-dimensional analysis of the relationship between periphyton biomass development in the study streams as a function of both disturbance frequency (floods $yr^{-1}$) and enrichment (as measured by % $N_C$). The surface was generated by a linear smoothing procedure (smooth = linear in SYGRAPH, Wilkinson 1990) based on the data in Tables 2.1 and 2.5.

## IV. Discussion

The potential importance of climate, and associated flood disturbance regimes, to the overall structuring of stream ecosystems has been highlighted in recent reviews (Minshall, 1988; Resh *et al.*, 1988; Poff & Ward, 1989; Townsend, 1989; Naiman *et al.*, 1992). Inorganic nutrient supplies (reflecting different catchment geology/landuse regimes) are also important driving variables for primary production, and potentially act in association with disturbance to set the overall habitat template for periphyton growth dynamics in streams. My results show there is great scope for further comparative studies across climatic boundaries that include contrasting geological and landuse regimes. Such studies will contribute significantly to our understanding of the disturbance-resource stress template of stream ecosystems. They will also assist with understanding broad scale changes in fluvial systems (Naiman *et al.*, 1992) within which more specific models, such as the River Continuum Concept (Vannote *et al.*, 1980), can be placed and adjusted to make them applicable in a greater range of biomes.

The hypothesis (see Introduction) that average periphyton biomass among streams is negatively correlated with disturbance frequency could not be rejected in the present study. Floods (frequency and velocity intensity) explained a very high amount of the variance in biomass, and catchment enrichment explained much of the remaining variance. My results support the concept that the main habitat axes can be defined by a gradient of disturbance and nutrient enrichment as has been depicted for terrestrial plants by Grime (1977). They also support the earlier study of Biggs & Close (1989) who concluded that flow regimes contribute at least equally with nutrients to differences in periphyton development among streams.

The susceptibility of periphyton to flood disturbances varies widely (e.g. Biggs & Close, 1989; Grimm & Fisher, 1989). Biomass loss depends on both the size of the flood, and the biomass, taxonomic structure, age, and physiological state of the pre-flood community (Biggs & Close, 1989; Grimm & Fisher, 1989; Peterson & Stevenson, 1992). Low biomass communities of prostrate diatoms, and/or taxa with specialised holdfast structures, appear to be most resistant to flood disturbance (e.g. Power & Stewart, 1987; Biggs & Close, 1989; Uehlinger 1991). In this study, a critical average velocity of 1 $ms^{-1}$ was set a-priori to signify conditions which would result in disturbance of the periphyton. Values in excess of this were expected to result in extensive sloughing. More recent experiments over a range of disturbance velocities have shown that an increase in mean water column velocity from < 0.3 m $s^{-1}$ to > 1m $s^{-1}$ can result in > 50 % sloughing of mature filamentous algal communities (dominated by *Melosira varians* and *Spirogyra* sp.) (see Chapter 3). When velocities exceeded 1.5 m $s^{-1}$ (which usually happens during flood flows; e.g. Fig. 2.3), > 70% of the community can be removed by water shear alone. This provides some empirical evidence to confirm that 1 m $s^{-1}$ was an appropriate flow threshold for defining a disturbance in this study.

A key effect of individual disturbances is the alteration of resource availability to plants (Grime, 1977; Pickett & White, 1985 p.383). In streams, floods may result in an increase, decrease or no change in nutrient concentrations in water depending to a major extent on the landuse of the catchment and frequency of events (see Humphrey & Stevenson, 1992; and references contained therein). With frequent high rainfall events, one would expect a depletion of the pool of mineralised nutrients in the soil profile through repeated leachings, resulting in reduced inter-flood stream water ion concentrations (e.g. Grimm & Fisher, 1992). This appears to occur in New Zealand, where strong negative relationships between the specific water yield of catchments and their low-flow ion (and some nutrient) concentrations have been demonstrated (Close & Davies-Colley, 1990). This feature has important implications for rates of periphyton community recovery (Pickett & White, 1985 p.380; Lohman *et al.*, 1992) and competition between species during inter-disturbance periods (Grime, 1977;

Stevenson *et al.*, 1991). Because resistance to disturbance is affected by biomass and successional state (Biggs & Close, 1989; Peterson & Stevenson, 1992), it also contributes to the longer term sensitivity of a habitat to further disturbance. Where resource levels are very low, only the severest of physical events will represent important re-setting disturbances because of low, resource stressed, biomass during the inter-disturbance periods. In the present study, catchments prone to frequent flood disturbance generally had lower background ion concentrations (as measured by conductivity, Table 2.4). Disturbance frequency may therefore affect stream periphyton by both physical detachment, and by affecting the nutrient status of the water. This suggests that the mean monthly biomass values recorded in this study were to some extent the result of an interaction between disturbance frequency and intensity, and nutrient availability processes. Thus, the climate-disturbance gradient will have a more important role in structuring stream ecosystems among biomes than has been appreciated in most previous studies which have focussed only on physical effects and ignored nutrient stress.

The stream water dissolved inorganic nutrient results appeared to invalidate my a-priori designation of sites into three enrichment groups. However, in shallow streams with gravel and cobble beds and large surface areas, periphyton mats, with their high nutrient uptake rates (Rutherford *et al.*, 1987), can greatly deplete nutrients in the water over short distances (e.g. McColl, 1974; Mulholland & Rosemond, 1992). Indeed, in some rivers significant negative correlations occur between temporal changes in periphyton biomass and dissolved inorganic nutrient concentrations (Biggs & Gerbeaux, 1993). In the present study, the site with the highest biomass of periphyton (280.8 mg $m^{-2}$ chlorophyll *a*, Maraekakaho River) had very similar average concentrations of nitrogen and phosphorus (Table 2.3) to the site with the lowest average biomass (2.1 mg $m^{-2}$ chlorophyll *a*, Waimana River). I strongly advocate the use of conductivity as an easy, relative, surrogate for enrichment in streams because the major ions that it represents are not subject to the same influence by biological processes (i.e. it is conservative), and there is ample basis to suggest that it reflects relative degrees of nutrient supply (Biggs 1988). In New Zealand, conductivity is correlated very strongly with geology and intensity of landuse (Close & Davies-Colley, 1990; see also Table 2.4 of this study), and Biggs & Price (1987, fig. 5), Biggs (1988, fig. 3), and Biggs (1990, fig. 3) have demonstrated very close relationships between the biomass and taxonomic composition of periphyton and low-flow conductivity. This parameter (conductivity), and the cellular nitrogen concentration of periphyton, which measures actual nutrient status of the plant communities, correlate strongly with the a-priori designation of the site enrichment groups in the present study (Table 2.3, Fig. 2.4).

The close nature of the relationships between chlorophyll *a* concentration and the 80th percentile velocity for the three enrichment groups (Fig. 2.8) was remarkable and suggests that average periphyton biomass over periods of a year or more could be predicted from these parameters. While classification of the sites into enrichment groups was done on the basis of catchment characteristics, it could also have been done on the basis of stream water conductivity (see Results for mean values for each group, and Biggs 1990). The minimal scatter around each line for the chlorophyll *a* - 80th percentile velocity relationship was probably due to the sites within each group having very similar levels of enrichment (as indicated by cellular N concentrations, Fig. 2.4) and similar dominant taxa. The robustness of this relationship was investigated by re-plotting the chlorophyll data against different velocity percentiles ranging from the 50th percentile (median in Table 2.1) to the 95th percentile. The degree of scatter increased as the percentile level was reduced, but the basic relationships held.

The different chlorophyll *a* - $V_{80}$ relationships in Fig. 2.8 for each enrichment group probably encompass differences in the relative degree of disturbance vs. nutrient limitation control. Communities at the nutrient rich sites are likely to be nutrient saturated and the level of biomass accrual will be more determined by physical limitations of velocity. However, the relationship for the moderate enrichment group at $V_{80}$ values of $< 0.8$ m $s^{-1}$ (the point where the upper and lower relationships converge) is probably defined by a combination of mat nutrient mass transfer limitation and velocity limitation. This gives a lower biomass for a given value of $V_{80}$ than for the associated enriched sites. For the unenriched sites, it is likely that the communities are under such extreme nutrient stress that little biomass develops during interflood periods and most floods have little opportunity to affect them.

The average taxonomic composition of stream periphyton communities across disturbance regimes showed a high degree of similarity (Table 2.5). Distinct differences occurred only after extended periods of low flow when proliferations of green filamentous algae developed at sites that were enriched (Table 2.6). At such times competition could become an important determinant of community structure (as suggested by Grime (1977) for terrestrial ecosystems). Active tolerance mechanisms of succession (Pickett *et al.*, 1987) may allow more aggressive competitors for nutrients and light to dominate (e.g. Peterson & Stevenson, 1990; McCormick & Stevenson, 1991; Stevenson *et al.*, 1991). However, diatoms, particularly *Gomphoneis herculeana*, *Synedra ulna* and *Cymbella kappii*, were present under many environments, and were abundant under most combinations of disturbance and enrichment.

Often nutrient limitation is viewed in relatively short, perhaps single season, time-frames (e.g. Hill & Knight, 1988) that may not reflect longer term conditions. Thus, temporal variability in limitation can occur (e.g. Bothwell, 1989) through changes in nutrient supply rates and/or changes in the structural characteristics of the community (e.g. Hudon *et al.*, 1987; Paul & Duthie, 1989). While averaging of cellular nutrient concentrations over the year does result in some loss of information, the value is that it enables the overall nutrient status of the communities and catchment conditions to be linked (Fig. 2.5). Evidence for nitrogen limitation of stream periphyton in many regions is growing (e.g. Triska *et al.*, 1983; Grimm & Fisher, 1986; Bushong & Bachman, 1989) and catchments dominated by P rich volcanic rocks (Grimm & Fisher, 1986) and high agricultural development (Bushong & Bachman, 1989) are generally N limited. The strong positive correlation between percentage of the catchment in high intensity agriculture and cellular N (but not cellular P) supports the conclusion based on cellular N concentrations and N:P ratios that N was probably the limiting nutrient at most sites in the present study.

Many studies have demonstrated seasonal shifts in the biomass of periphyton in gravel-bed rivers, with spring and fall maxima (e.g. Biggs & Close, 1989; Uehlinger, 1991; Lohman *et al.*, 1992). However, the occurrence of such seasonal patterns can now been viewed in a wider perspective of flood disturbance frequency. Biggs & Close (1989) suggested that seasonal cycles would be truncated in disturbance-prone streams, and that well-defined patterns of seasonality should occur only in, and are indictive of, low frequency disturbance regimes. The present study from a much wider array of streams, covering a variety of geographic regions, provides further support for this contention.

The effects of invertebrate grazing on periphyton development were not considered in this study. It can be an important factor controlling periphyton biomass accrual in natural streams (e.g. Rosemond *et al.*, 1993), particularly where streams have low nutrient inputs, stable bed sediments, and infrequent floods (e.g. Biggs & Lowe, 1994). However, none of the streams in the present study had these characteristics. Those which had few floods tended to be enriched and as a result had high periphyton production which appeared to greatly exceed grazer consumption.

There has been much discussion on the potential to array streams along axes that correspond to gradients in climate, and associated disturbance regimes, in order to explain broadscale differences in ecosystem structure (Minshall *et al.*, 1985; Minshall, 1988; Poff & Ward, 1989; Townsend, 1989; Naiman *et al.*, 1992). The present study provides empirical support for the concept that disturbance frequency is a fundamental discriminator of habitats for stream periphyton. My results suggest that: (1) the climate/flood disturbance regime is a primary axis of the habitat template for

periphyton, and (2) nutrient resources operate within this by controlling the rate of biomass accrual during periods of stable flow. It is also apparent that the flow variability regime can strongly influence nutrient supply to streams. Thus, differences in flood frequency among streams, in combination with various levels of enrichment, have the potential to explain biomass development in periphyton communities within large geographic regions. The disturbance - resource stress template provides the axes along which the structure and function of many temperate latitude streams can be arranged and compared.

## V . Summary

Periphyton chlorophyll *a*, ash-free dry mass, taxonomic composition, and cellular and water-column nutrients were analysed every 4 weeks for a year at 16 sites. Overall, mean monthly chlorophyll *a* concentration declined with increasing flood frequency ($r$ = -0.711, $P$<0.001), and seasonality in chlorophyll *a* was better defined at sites with a low frequency of floods. Chlorophyll *a* concentration was generally low throughout the year at sites with frequent floods (> 15 $yr^{-1}$).

No relationship existed between inorganic nutrient concentrations and catchment geology or land development. However, conductivity declined significantly as a function of the percentage of the catchment underlain by nutrient poor, hard rocks (plutonic and fine grained metamorphic rocks) ($r$ = -0.515, $P$ <0.05), but increased significantly with the percentage of the catchment in intensive agricultural landuse ($r$ = 0.799, $P$ < 0.001). Cellular nutrient concentrations suggested that nitrogen was the nutrient most commonly limiting periphyton production. In turn, cellular N concentrations declined significantly with increasing percentage of the catchment in hard rock ($r$ = -0.561, $P$ < 0.05) and increased with percentage of the catchments in intensive agricultural landuse ($r$ = 0.948, $P$ < 0.001). The sites were classified into three enrichment groups (high, moderate and low) based on their landuse and underlying geology. Cellular N concentrations varied significantly among these enrichment groups (ANOVA F = 14.661, $P$ < 0.001).

Log chlorophyll *a* decreased significantly with increases in the annual 80th percentile velocity. However, the relationship was significantly different among the enrichment groups. A stepwise multiple regression on the full dataset identified that the frequency of floods, proportion of the catchment in high intensity agricultural landuse, and proportion of the catchment in alkaline rocks were the most significant factors explaining variation in mean monthly chlorophyll *a* among the sites ($r^2$ = 89 %). Overall, the results showed that flood disturbance and catchment enrichment regimes are probably the principal axes of the habitat template of periphyton among the study

streams, and could be used to explain and predict broadscale differences in periphyton development among other temperate stream ecosystems.

## VI . References

Auer M.T. & Canale R.P. (1982) Ecological studies and mathematical modelling of *Cladophora* in Lake Huron. 3. The dependence of growth rates on internal phosphorus pool size. *Journal of Great Lakes Research*, **8**, 93-99.

Biggs B.J.F. (1982) Effects of low flow regulation on river water quality and biology: a case study. *River low flows: conflicts of water use* (Ed. R.H.S. McColl), pp. 28-44. Ministry of Works and Development.

Biggs B.J.F. (1988) Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1405-1411.

Biggs B.J. (1990) Periphyton communities and their environments in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 367-386.

Biggs B.J.F. (1994) Hydraulic habitat of plants in streams. *Proceedings of the 1st International Symposium on Habitat Hydraulics, Trondheim, Norway, 1994* (Ed. K.A. Vaskin), pp. 411-429. International Association of Hydraulics Research and The Norwegian Institute of Technology.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs B.J.F., Duncan M.J., Jowett I.G., Quinn J.M., Hickey C.W., Davies-Colley R.J. & Close M.E. (1990) Ecological characterisation, classification and modelling of New Zealand rivers: an introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research*, **24**, 277-304.

Biggs B.J.F. & Gerbeaux P. (1993) Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **27**, 39-53.

Biggs B.J.F. & Lowe R.L. (1994) Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *New Zealand Journal of Marine and Freshwater Research*, **28**, 119-134.

Biggs B.J.F. & Price G.M. (1987) A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **21**, 175-191.

Boston H.L. & Hill W.R. (1991) Photosynthesis-light relations of stream periphyton communities. *Limnology and Oceanography*, **36**, 644-656.

Bothwell M.L. (1988) Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 261-270.

Bothwell M.L. (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1293-1301.

Bourelly P. (1990) *Les Algues D'eau Douce: Initiation ala systematique,Tome 1.* Les Algues Vertes Boubee.

Bushong S.J. & Bachman R.W. (1989) In situ nutrient enrichment experiments with periphyton in agricultural streams. *Hydrobiologia*, **178**, 1-10.

Close M.E. & Davies-Colley R.J. (1990) Baseflow water chemistry in New Zealand rivers. 2. Influence of environmental factors. *New Zealand Journal of Marine and Freshwater Research*, **24**, 343-356.

Cooper A.B., Hewitt J.E. & Cooke J.G. (1987) Land use impacts on streamwater nitrogen and phosphorus. *New Zealand Journal of Forestry Science*, **17**, 179-192.

Dillon P.J. & Kirchner W.B. (1975) The effects of geology and land use on the export of phosphorus from watershed. *Water Research*, **9**, 135-148.

Feminella J.W. & Resh V.H. (1990) Hydrologic influences, disturbances, and intraspecific competition in a stream caddisfly population. *Ecology*, **71**, 2083-2094.

Fisher S.G. & Grimm N.B. (1988) Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1183-1190.

Foged N. (1979) *Diatoms in New Zealand, the North Island.* Cramer. 225p.

Griffiths G.A. & McSaveney M.J. (1983) Distribution of mean annual percipitation across some steepland regions of New Zealand. *New Zealand Journal of Science*, **26**, 197-209.

Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169-1194.

Grimm N.B. & Fisher S.G. (1986) Nitrogen limitation in a Sonoran Desert stream. *Journal of the North American Benthological Society*, **5**, 2-15.

Grimm N.B. & Fisher S.G. (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, **8**, 292-307.

Grimm N.B. & Fisher S.G. (1992) Responses of arid-land streams to changing climate. *Global Climate Change and Freshwater Ecosystems* (Eds. P. Firth & S.G. Fisher), pp. 211-233. Global Climate Change and Freshwater Ecosystems, Springer-Verlag.

Hill A.R. (1978) Factors affecting the export of nitrate-nitrogen from drainage basins in southern Ontario. *Water Research*, **12**, 1045-1057.

Hill W.R., Boston H.L. & Steinman A.D. (1992) Grazers and nutrients simultaneously limit lotic primary productivity. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 504-512.

Hill W.R. & Knight A.W. (1988) Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology*, **24**, 125-132.

Horner R.R., Welch E.B., Seeley M.R. & Jacoby J.M. (1990) Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology*, **24**, 215-232.

Hudon C., Duthie H.G. & Paul B. (1987) Physiological modifications related to density increase in periphytic assemblages. *Journal of Phycology*, **23**, 393-399.

Humphrey K.P. & Stevenson R.J. (1992) Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates. *Journal of the North American Benthological Society*, **11**, 37-48.

Jowett I.G. & Duncan M.J. (1990) Flow variability in New Zealand rivers and its relationship to instream habitat and biota. *New Zealand Journal of Marine and Freshwater Research*, **24**, 305-318.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores; experimental study of grazing by a caddisfly population. *Ecology*, **64**, 1124-1135.

Lohman K., Jones J.R. & Perkins B.D. (1992) Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1198-1205.

McColl R.H.S. (1974) Self-purification of small freshwater streams: phosphate, nitrate, and ammonia removal. *New Zealand Journal of Marine and Freshwater Research*, **8**, 375-388.

McCormick P.V. & Stevenson R.J. (1991) Mechanisms of benthic algal succession in lotic environments. *Ecology*, **72**, 1835-1848.

McElravy E.P., Lamberti G.A. & Resh V.H. (1989) Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society*, **8**, 51-63.

Ministry of Works and Development (1979) *Our land resources - a bulletin to accompany the New Zealand Resources Inventory Worksheets*. Government Printer. 79p.

Minshall G.W. (1988) Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263-288.

Minshall G.W., Cummins K.W., Petersen R.C., Cushing C.E., Bruns D.A., Sedell J.R. & Vannote R.L. (1985) Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **42**, 1045-1055.

Mosley M.P. (1983) Response of braided rivers to changing discharge. *Journal of Hydrology (NZ)*, **22**, 18-67.

Mulholland P.J. & Rosemond A.D. (1992) Periphyton response to longitudinal nutrient depletion in a woodland stream: evidence of upstream-downstream linkage. *Journal of the North American Benthological Society*, **11**, 405-419.

Naiman R.J., Longarch D.G., Beechie T.J. & Ralph S.C. (1992) General principles of classification and the assessment of conservation potential in rivers. *River Conservation and Management* (Eds. P. J. Boon, P. Calow & G.E. Petts). John Wiley and Sons.

Omernik J.M. (1977) *Nonpoint source - stream nutrient level relationships: a nationwide study.* US-EPA 600/3-77-105. 151p.

Patrick R. & Reimer C.W. (1966) *The diatoms of the United States. Vol 1.* Academy of Natural Sciences. 688p.

Patrick R. & Reimer C.W. (1975) *The diatoms of the United States. Vol. 2.* Academy of Natural Sciences. 213p.

Paul B.J. & Duthie H.C. (1989) Nutrient cycling in the epilithon of running waters. *Canadian Journal of Botany*, **67**, 2302-23090.

Peterson C.G. & Stevenson R.J. (1990) Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Botany*, **68**, 2092-2102.

Peterson C.G. & Stevenson R.J. (1992) Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*, **73**, 1445-1461.

Pickett S.T.A., Collins S.L. & Armesto J.J. (1987) Models, mechanisms and pathways of succession. *The Botanical Review*, **53**, 335-371.

Pickett S.T.A. & White P.S. (1985) Patch Dynamics: a synthesis. *The Ecology of Natural Disturbance and Patch Dynamics* (Eds. S.T.A. Pickett & P.S. White), pp. 371-384. Academic Press.

Poff N.L. (1992) Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society*, **11**, 86-92.

Poff N.L. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805-1818.

Power M.E. & Stewart A.J. (1987) Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist*, **117**, 333-345.

Prescott G.S. (1973) *Algae of the Western Great Lakes areas*. Wm C Brown. 977p.

Prescott G.W. (1981) *How to know the freshwater algae*. Wm C Brown Company Publishers.

Quinn J.M. & Hickey C.W. (1990) Magnitude of effects of substrate particle size, recent flooding and catchment development on benthic invertebrate communities in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 411-427.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Hiram W.L., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance instream ecology. *Journal of the North American Benthological Society*, **7**, 433-455.

Robinson C.T. & Minshall G.W. (1986) Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society*, **5**, 237-248.

Rosemond A.D., Mullholland P.J. & Elwood I.W. (1993) Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology*, **74**, 1264-1280.

Rutherford J.C., Williamson R.B. & Cooper A.B. (1987) Nitrogen, phosphorus and oxygen dynamics in rivers. *Inland waters of New Zealand* (Ed. A.B. Viner). NZ Department of Scientific and Industrial Research.

Sartory D.P. & Grobelaar J.E. (1984) Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, **114**, 177-187.

Stevenson R.J., Peterson C.G., Kirschtel D.B., King C.C. & Tuchman N.C. (1991) Density-dependent growth, ecological strategies and effects of nutrients and shading on benthic diatom succession in streams. *Journal of Phycology*, **27**, 59-69.

Suggate R.P. & Riddolls P.M. (1976) Geology. *New Zealand Atlas* (Ed. I. Ward). NZ Government Printer.

Timperley M.H. (1983) Phosphorus in spring waters in the Taupo volcanic zone, North Island, New Zealand. *Chemical Geology*, **38**, 287-306.

Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36-50.

Triska F.J., Kennedy V.C., Avangino R.J. & Reilly B.N. (1983) Effect of simulated canopy cover on the regulation of nitrate uptake and primary production by natural periphyton assemblages. *Dyamics of Lotic Ecosystems* (Eds. T.D. Fontaine & S.M. Bartell). Ann Arbor Lisense.

Uehlinger U. (1991) Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv fur Hydrobiologie*, **123**, 219-237.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.

Whitford L.A. & Schumacher G.J. (1973) *A manual of freshwater algae*. Spars Press. 324p.

Wilkinson L. (1990) *SYSTAT: The system for statistics*. SYSTAT Inc.

Winterbourn M.J. (1990) Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology*, **23**, 463-474.

# Chapter 3

## Disturbance of stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistance

**Preface**

In the previous chapter, I established a significant negative relationship between flood disturbance frequency and average periphyton biomass in streams. However, there was much variability in this relationship. In particular, I found that periphyton biomass in high nutrient supply environments was strongly related to disturbance frequency whereas biomass in low nutrient supply environments was only poorly related to disturbance frequency. I hypothesize that these differences in disturbance effects are probably a result of differences in disturbance resistance of the taxa dominating the communities under different degrees of enrichment (filamentous taxa in moderate - highly enriched streams vs. adnate diatoms in unenriched streams). In the following chapter, I investigate this hypothesis by determining the shear stress required to remove from the streambed varying proportions of two filamentous and two diatom dominated periphyton communities. The study was carried out by incubating large (0.4 x 0.6m) duplicate artificial substrates (consisting of plastic sheets, blow moulded so that the surface was covered in 2 cm diameter hemispheres to simulate a gravelbed) in four streams differing in nutrient supply to obtain the test communities. The substrates were then transported back to the lab and subjected to a gradient of increasing shear stress (1 - 90 $N.m^{-2}$) in a flow tank. The amount of periphyton removed from the substrata was then determined from sequential measurements of chlorophyll *a* in the overlying waters. A preliminary experiment was carried out with one of the communities to determine the time it takes to start sloughing once it is subjected to an elevation in shear stress. This was followed by a second experiment with all four communities to determine the kinetics of loss as a function of shear stress and degree of resistance of the different communities. This study has now been published in the *Journal of Phycology* **31**:233-241.

## I. Introduction

A variety of factors are important to periphyton development on stones in streams (see Chapter 1). Differences in the frequency/intensity of disturbance by spates may be the major mechanism controlling among stream differences in biomass as shown in Chapter 2 (see also Tett et al. 1978, Biggs 1988, Fisher and Grimm 1988, Biggs and Close 1989, Power 1992). Indeed, Steinman et al. (1990) stress that the type and duration of a disturbance may be more important to stream ecosystem behaviour than factors such as nutrient levels or plant/animal interactions which have been considered fundamental previously.

Field studies described in Chapter 2 have shown that the degree that disturbance effects the periphyton varies among streams with different degrees of enrichment. Further, other studies have shown that the loss of biomass for a given community is not a linear function of spate intensity (Biggs and Close 1989). These factors create difficulties in predicting the extent and timing of disturbance of the periphyton from measurement of variables such as stream flow. Also, modelling of temporal changes in biomass will be difficult since different degrees of loss with given intensity events will have major effects on rates of regeneration. For example, exponential growth could occur in communities soon after a spate if destruction has only been partial, whereas immigration/colonization is a pre-requisite for community re-establishment if complete destruction of the community has occurred. The overall result of these effects will be that periphyton data obtained from individual samplings in streams prone to spates will be difficult to explain in terms of other environmental variables (e.g. light, nutrients, grazing etc.) (e.g. Smith and Maasdam 1994).

Many factors appear to contribute to the varying degrees of loss of periphyton during spates. These are the communities' resistance properties and can be classified into two main types: "inherent" and "conditional". Inherent properties relate to the physical attributes of the dominant populations and include their shape, size, texture, tensile strength, and attachment strength. Conditional properties relate more to the association of a community with its environment. These include its age, the occurrence of secondary substrates, and acclimation to a given shear stress and/or resource conditions. Here I focus on inherent properties only.

The degree of drag to which a periphytic cell, or filament, is subjected as shear stress increases with the commencement of a spate, relates both to skin friction (determined by the roughness of the surface and the length of surface exposed to the current) and form drag (determined by the size of the cross-sectional area against which the current collides). The drag on small organisms is mainly due to skin friction. However, for larger (and more upright) organisms form drag tends to be much greater and the magnitude of this drag grows in proportion to the square of the velocity (Koehl 1982). Thus, empirical studies have recognized that some low profile diatoms which dominate the communities of unenriched streams (e.g. *Achnanthidium minutissimum* and *Cocconeis placentula*) have considerable resistance to hydraulic disturbance (e.g. Rounick and Gregory 1981, Luttenton and Rada 1986, Robinson and Rushforth 1987, Horner et al. 1990, Peterson and Stevenson 1992). Conversely, attached filamentous taxa, with their much higher surface area (which increases skin friction), and cross-sectional areas (which increases form drag), which dominate the communities of enriched streams are expected to be more susceptible to elevations in shear stress. No studies have specifically tested this although Grimm and Fisher (1989) showed that diatoms were considerably more resistant than filamentous green algae to spates in a Sonoran Desert stream where both shear stress sloughing and sediment abrasion occurred, and Uehlinger (1991) observed that filamentous algae were slightly less resistant to bed moving floods than non-filamentous forms in a Swiss pre-alpine river. Furthermore, in an experimental trough study, Horner et al. (1990) found that velocity elevation (from 20 to 80 $cm.s^{-1}$) changed community dominance from the filamentous taxa *Phormidium* sp. and *Mougeotia* sp. to dominance by the diatoms *Fragilaria* sp. and *Synedra* sp., suggesting that the latter (generally non-filamentous) taxa were more resistance to velocity increases.

In this chapter I describe a set of laboratory experiments which more fully quantify the degree to which different periphyton communities are resistant to hydraulic disturbance. The specific objectives were to: 1) investigate how long a community can resist the effects of differing magnitude increases in shear stress to determine whether there is a time component to inherent resistance (e.g. is a flow perturbation with a long duration likely to be more of a disturbance than a short-duration event ?); 2) compare the degree of sloughing for two non-filamentous (diatom) and two filamentous periphyton communities with incremental increases

in shear stress; and 3) determine the specific shear stresses required to remove given quantities of biomass for different community types.

Through this I also wished to address the wider question of whether the structurally more complex filamentous communities of enriched streams had a lower resistance to spates than non-filamentous communities of unenriched streams, and so provide a basis for interpreting the likely impact of spates of different intensities in streams. The confounding effects of physical abrasion by bed sediment movement during very high flows are not considered here.

## II. Materials and Methods

My study was conducted in the flowtank laboratory, National Institute of Water and Atmospheric Research, Christchurch (South Island, New Zealand). In brief, the tank was 1.5 m long and 0.4 m wide, had a volume of 196.8 litres and was made of 16 mm thick plexiglass. It was a much enlarged, and somewhat modified, version of that described by Lacoursiére and Craig (1990). An upper test section was 0.2 m deep, and a lower test section was 0.1 m deep. The water (untreated, high quality aquifer water) was recirculated in a closed-off loop enabling cumulative changes in the concentration of suspended organic matter to be monitored for determining the degree of sloughing from test substrata. Twin, 0.17 m diameter, 3-bladed, motor boat propellers were connected via a pulley-notch belt system to a 3 hp (2.2 kW) motor to provide the driving force for water movement. Maximum free stream velocities of up to 1.2 $m.s^{-1}$ were possible in the upper test section and 2.4 $m.s^{-1}$ in the lower section.

To determine values for mean shear stress ($\tau$), velocity profiles were measured for a series of motor settings at (generally) 2 mm depth intervals above the bed (upper panel, Fig. 3.1) using a calibrated hot film anemometer (Model TSI1750 with rugged side-flow probe). Individual readings were carried out for periods of >1 min duration. From these profiles, the depth values were logged and regressed against velocity from the log-linear part of the velocity profile (lower panel, Fig. 3.1). The resultant regression coefficient was then used to calculate shear velocity ($U_*$) (after Gordon et al. 1992) as:

$$U_* = \frac{b}{5.75} \qquad (1)$$

where $b$ is the slope of the logarithmic velocity profile (velocity vs. log depth). $U_*$ is inversely proportional to the gradient of velocity (in the boundary layer; Fig. 3.1) and consequently it has the dimensions of velocity ($m.s^{-1}$). Shear stress ($\tau$ in $Newtons.m^{-2}$) was calculated as:

$$\tau = \rho\,(U_*)^2 \qquad (2)$$

where $\rho$ is the density of water ($kg.m^{-3}$).

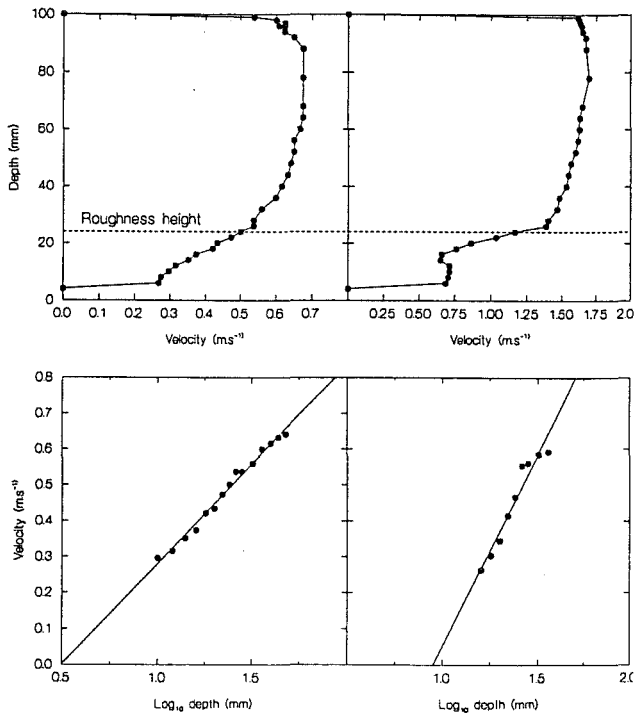


Fig. 3.1 Velocity profiles in the flow tank, measured using hot-film anemometry for two different flow settings. The height of the artificial substratum hemispheres is depicted on the upper panels as "roughness height". The upper panels also show the distribution of velocity through the depth of the streamflow, and the lower panels show these same data with velocity as a function of $\log_{10}$ of depth for the logarithmic region of the profile (i.e. <40 mm from the bed). The relationship in the lower panel was used to calculate shear stress for different flow settings in the tank.

An artificial cobble substatrum, which mimiced natural cobbles, was made of moulded plastic and fixed to a plexiglass sheet. These 0.24 $m^2$ (0.4 m x 0.6 m) substrata consisted of 4 cm diameter hemispheres (i.e. a roughness height of 2.5 cm, Fig. 3.1), with 199 hemispheres per substratum. I used textured plastic for the hemispheres to aid periphyton colonisation and somewhat represent the rough surface texture of crystaline stones. Two replicate substrata were used in all experiments. Colonisation of individual substrate was generally very uniform (mean % CV of 14.3 for triplicate samples of chlorophyll *a* from 13 substrata) and the between-substratum variability for initial communities was also low (mean % CV of 14.2 for 5 substrate incubated under the same velocities for 7 days).

*Time dependency of sloughing*

Four pairs of substrata were introduced on consecutive days at the same locality in the moderately enriched Cust River, Canterbury-New Zealand, and incubated for 7 days. Velocity profiles were measured above each substratum using a small Ott-current meter to ensure that the pairs were incubated under the same hydraulic conditions. After seven days both substrata were retrieved and transported to the laboratory in sealed plastic boxes with a small amount of water in the bottom of the boxes to keep the atmosphere humid. Substrata could not be transported submersed in water because oscillations dislodged material. Substrate were kept like this for <2 h before each experiment commenced with no obvious detrimental effect on the communities. Immediately before installing the substrata in the flow tank, three hemispheres were scraped using a toothbrush and scalpel to obtain samples for initial analyses of chlorophyll *a* and ash-free dry mass (AFDM) concentrations. Once a substratum was installed in the tank (lower test section), it was filled with water and the community was exposed to a pre-determined level of shear stress for 90 minutes. Every 10 min a new sampling round commenced with six 60 mL replicates of water being removed from the recirculating water using a syringe attached to a 7 mm diameter stainless steel tube penetrating into the water column. Three replicates were analysed for chlorophyll *a* and the other three for AFDM. The sloughed material was fully homogenised in the water by the propellers driving the water flow. After 90 min exposure to a particular treatment the substratum was removed from the flow tank, and three hemispheres were scraped clean and analysed for any remaining biomass as for the initial samples. Each shear stress treatment was repeated with a second substratum. Pairs of substrata were exposed to one of the following shear stress levels: 4.5, 5.3, 16.9 or

25.6 $N.m^{-2}$, so that a range that could be expected in a stream during normal spates was evaluated (calculated from data in Hicks and Mason 1991).

The percentage biomass sloughed from the substrata at each shear stress level was calculated by comparing the cumulative mass of organic matter in the water at each sampling time to the initial mass present on the substrata.

*Sloughing as a function of community type*

Pairs of substrata were incubated for 14 days under approximately the same hydraulic conditions, but in four different gravel-cobble bed streams to obtain different community types of similar ages.

At the completion of the incubation, each pair of substrata was transported to the laboratory and initial samples were removed as described above. The shear stress required to slough the accrued periphyton was determined for each replicate by driving water through the flow tank at increasing increments of shear stress (between 1.0 and >90 $N.m^{-2}$). After 5 min of each treatment, six 60 ml replicate samples of water were taken for analysis of chlorophyll *a* (three replicates) and AFDM (the other three replicates). The community was exposed to each shear stress treatment for a total of 10 minutes. After the experiment, three hemispheres were scraped clean. The pre- and post-treatment samples were homogenized and sub-sampled for analyses of chlorophyll *a*, AFDM, and taxonomic composition.

For this experiment the data were analysed in two ways. First, community biomass and the relative abundance of taxa were compared before and after the full range of shear-stress treatments to determine overall differences in resistance. Second, cumulative biomass loss was plotted as a function of each shear stress increment to identify differences in loss kinetics between communities. From this, estimates of shear stresses necessary to dislodge specific amounts of biomass from the communities were obtained.

*Laboratory analyses*

AFDM was determined by filtering replicate samples through Whatman GFC filters. The samples were dried for 24 h at 105°C, weighed, ashed for four h at 440°C, and

reweighed. The samples were cooled in a desiccator before each weighing. Chlorophyll *a* was determined by extraction in boiling (78°C) 90% ethanol for 5 min and steeping in the dark at 4°C for 24 h (Sartory and Grobelaar 1984). Absorbance was measured at 665 nm and 750 nm on a spectrophotometer. Acidification was used to correct for phaeopigments, and a chlorophyll *a* coefficient of 28.66 was used. All analyses are expressed in units.$m^{-2}$. All samples, including samples of the water from the flow tank, were stored chilled and processed within 36 hours.

The relative abundances of taxa were assessed using a compound microscope (maximum magnification, 800x) and a haemocytometer. For the experiment investigating time dependency of sloughing, a "quick scan" was conducted to assess general taxonomic structure of communities. However, for the experiment investigating sloughing as a function of community type, a full quantitative analysis was performed. At least 200 cells were enumerated on samples of initial and final periphyton communities for each replicate using a strip counting procedure.

## III. Results

*Duration of resistance under different shear stresses*

The dominant taxon in this experiment was the filamentous diatom *Melosira varians*, with *Gomphonema parvulum* and *Cymbella minuta* also abundant. The combination of these taxa resulted in a community consisting of a slightly "fluffy" brown mat underlying masses of filaments which extended downstream for several centimetres from each substratum hemisphere. All communities were incubated at a mean velocity of 0.42 - 0.44 $m.s^{-1}$ and shear stresses fell within the narrow range of 2.4 $N.m^{-2}$ to 3.1 $N.m^{-2}$. Biomass was lost instantly when the communities were exposed to any of the given shear stress treatments. Also, the degree of biomass loss increased as a function of increasing shear stress (Fig. 3.2). The substrata exposed to a shear stress of 4.5 $N.m^{-2}$ experienced a mean chlorophyll *a* and AFDM loss of 19% and 32%, respectively; the substrata exposed to a shear stress of 5.3 $N.m^{-2}$ lost 28% chlorophyll *a* and 32% AFDM; the substrata exposed to a shear stress of 16.9 $N.m^{-2}$ lost 73% chlorophyll *a* and 64% AFDM; and the substrata exposed to a shear stress of 25.6 $N.m^{-2}$ lost 77% chlorophyll *a* and 86% AFDM.

Regression statistics for percentage loss vs. time of the pooled substratum data for each shear stress treatment (Table 3.1) showed that the change in biomass sloughed with time for most substrata was not significantly different from zero ($P > 0.05$). However, the relationship between chlorophyll biomass sloughed and exposure time for the 5.3 and 16.9 $N.m^{-2}$ treatments deviated from this ($P < 0.05$), although one was negative and the other positive.

*The effect of community structure on resistance*

The shear stresses under which the four substrata were incubated in the different streams ranged from 1.0 to 1.5 $N.m^{-2}$, depth ranged from 0.20 to 0.25 m and mean water column velocities from 0.41 to 0.46 $m.s^{-1}$. These velocities approximate the median column velocity for New Zealand gravel-cobble bed streams during median flow conditions (Biggs et al. 1990). Despite these similarities in physical parameters, four distinctly different communities developed, two dominated by adnate diatoms and two dominated by filamentous taxa (Table 3.2). The diatom dominated communities formed a low profile, tightly bound, mat whereas the communities dominated by filamentous algae were less dense with filaments extending for several centimetres in the flow downstream of the substratum hemispheres.

While all communities were of the same age (14 days), they varied widely in biomass (Table 3.2) reflecting differences in net production among the streams from which they were obtained. Of the two filamentous communities, one had the lowest and the other the highest initial chlorophyll *a* concentration.

Major sloughing of all communities occurred as a result of being exposed to a shear stress of 91.8 $N.m^{-2}$ (Table 3.2). A nested ANOVA (Table 3.3) indicated that for three of the test communities there was no between-replicate substratum differences in chlorophyll *a*, but that the differences in chlorophyll *a* as a function of shear stress were all significant ($P<0.02$). For the *Melosira varians* dominated community there was a significant difference in response between the two replicate substrata.

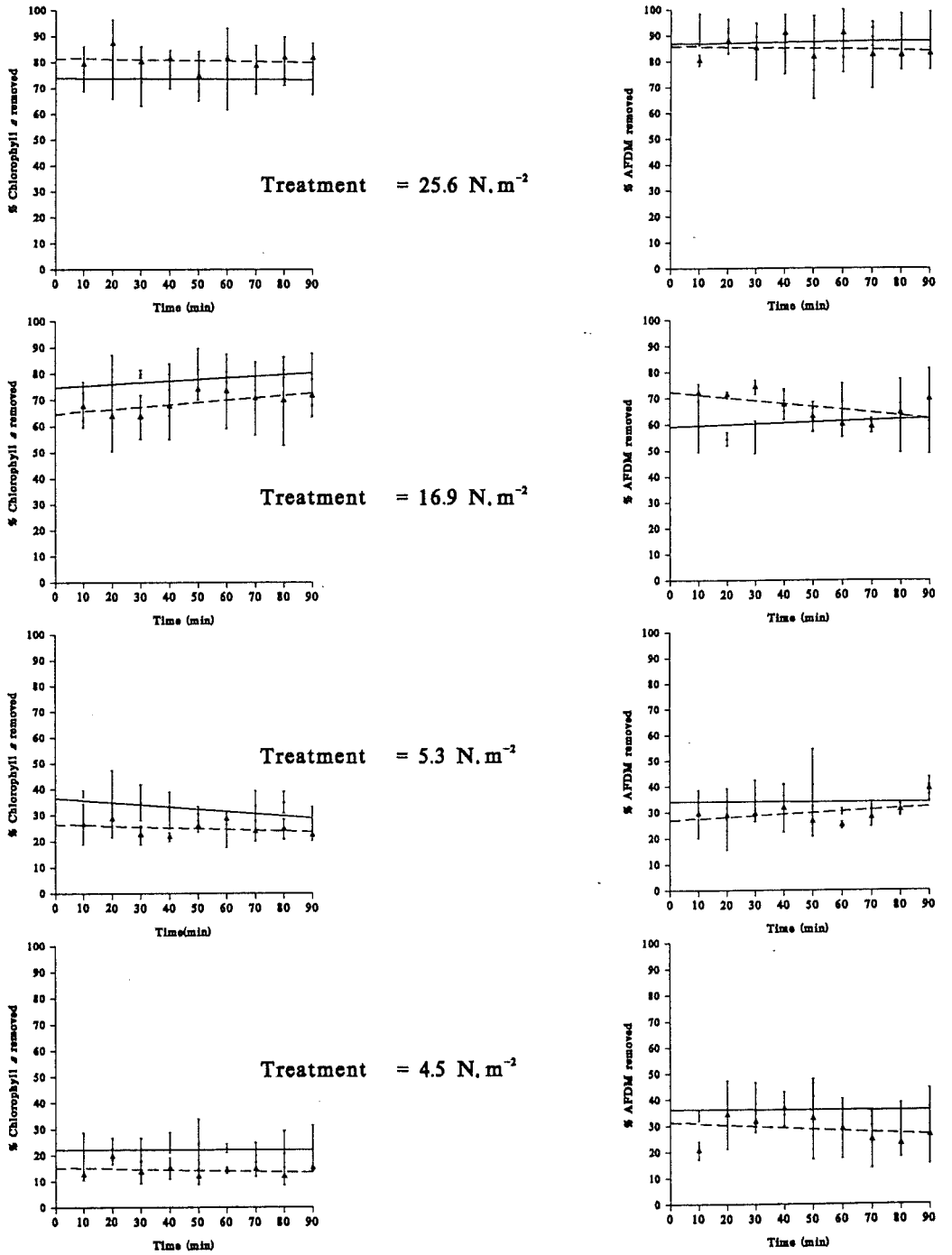


Fig. 3.2 Percent chlorophyll *a* (left panels) and ash-free dry mass (right panels) sloughed from the substrata over time under four different shear stress treatments. Error bars are standard errors. Solid lines and dots represent replicate substratum 1, and dashed lines and triangles represent replicate substratum 2.

Table 3.1 Linear regression statistics describing the relationship between percentage change in chlorophyll *a* and AFDM, and exposure time to different levels of shear stress.

| Shear stress ($N\ m^{-2}$) | Chlorophyll *a* | | Ash-free dry mass | |
|---|---|---|---|---|
| | Slope | *P* | Slope | *P* |
| 4.5 | -0.009 | 0.678 | -0.029 | 0.587 |
| 5.3 | -0.059 | 0.046 | 0.029 | 0.537 |
| 16.9 | 0.077 | 0.040 | -0.038 | 0.234 |
| 25.6 | -0.011 | 0.617 | -0.003 | 0.904 |

The degree of biomass loss (determined as percentage reduction in chlorophyll *a*) during the experimental treatment varied significantly among the communities (one-way ANOVA with two replicates per community; $P = 0.034$). The filamentous communities had the highest proportional loss, averaging 75% for the *Spirogyra* dominated community and 72% for the *Melosira* community. This compares with 44% for the *Fragilaria vaucheriae* and 62% for the *Fragilaria construens* dominated diatom communities. A Tukey multiple range test indicated that the difference in loss between the *Melosira varians* and *Fragilaria vaucheriae* communities were statistically different ($P = 0.017$), as was difference in loss between the *Spirogyra* sp. and *Fragiliaria vaucheriae* communities ($P = 0.012$).

An analysis of co-variance (Table 3.4) showed that the initial biomass concentration (Table 3.2) also influenced the degree of sloughing with communities of high biomass having a greater propensity to slough than low biomass communities. Once initial biomass was accounted for in the ANOVA, the differences in sloughing among the communities were much more significant ($P = 0.012$ for the among community ANOVA *vs.* $P = 0.002$ for when initial chlorophyll *a* was a co-variate). Community type explained 92% of the variance in sloughing (*vs.* 6.6% for initial biomass). Since the degree of resistance is given by the inverse of the

Table 3.2 Summary statistics for chlorophyll *a* and AFDM from the four periphyton communities analysed before (initial) and following (after) the maximum shear stress treatment. The statistics are calculated as the arithmetic mean ($\bar{x}$) and standard deviation (S.D.) from two test substrata for each community.

| Community | Treatment | Statistic | Chlorophyll *a* ($mg.m^{-2}$) | AFDM ($g.m^{-2}$) |
|---|---|---|---|---|
| Non-filamentous diatom dominated communities | | | | |
| A - *Fragilaria vaucheriae* | initial | $\bar{x}$ | 48 | 20 |
| *Cymbella minuta* | | S.D. | 2.0 | 0.5 |
| | after | $\bar{x}$ | 27 | 12 |
| | | S.D. | 1.0 | 0.8 |
| B - *Fragilaria construens* | initial | $\bar{x}$ | 60 | 23 |
| *Cymbella minuta* | | S.D. | 7.0 | 5.9 |
| *Achnanthidium minutissimum* | after | $\bar{x}$ | 23 | 5.1 |
| | | S.D. | 0.9 | 0.3 |
| Filamentous algal dominated communities | | | | |
| C - *Spirogyra* sp. | initial | $\bar{x}$ | 25 | 10 |
| *Gomphoneis herculeana* | | S.D. | 0.1 | 1.1 |
| *Ulothrix zonata* | after | $\bar{x}$ | 6.3 | 1.2 |
| | | S.D. | 0.9 | 0.04 |
| D - *Melosira varians* | initial | $\bar{x}$ | 98 | 17 |
| *Gomphonema parvulum* | | S.D. | 22 | 3.6 |
| | after | $\bar{x}$ | 27 | 9.9 |
| | | S.D. | 2.3 | 3.4 |

Table 3.3 Nested analysis of variance of chlorophyll *a* concentration associated with four different periphyton communities where "Treatment" is the effect of the maximum shear stress treatment, and "Substrata" represents the field replication (2 substrata for a given community subject to the "Treatment" with 3 replicate samples per substratum).

| Community | | Source | S.S. | DF | F-ratio | P |
|---|---|---|---|---|---|---|
| Non-filamentous diatom dominated | | | | | | |
| A - | *Fragilaria vaucheriae* | Treatment | 1186 | 1 | 11.208 | 0.012 |
| | *Cymbella minuta* | Substrata (Treatment) | 12 | 2 | 0.058 | 0.945 |
| | | Error | 741 | 7 | | |
| B - | *Fragilaria construens* | Treatment | 4180 | 1 | 21.305 | 0.002 |
| | *Cymbella minuta* | Substrata (Treatment) | 151 | 2 | 0.386 | 0.692 |
| | *Achnanthidium minutissimum* | Error | 1570 | 8 | | |
| Filamentous dominated | | | | | | |
| C - | *Spirogyra* sp. | Treatment | 1009 | 1 | 268.964 | 0.000 |
| | *Gomphoneis herculeana* | Substrata (Treatment) | 2.5 | 1 | 0.335 | 0.725 |
| | *Ulothrix zonata* | Error | 30 | 8 | | |
| D - | *Melosira varians* | Treatment | 12064 | 1 | 93.395 | 0.000 |
| | *Gomphonema parvulum* | Substrata (Treatment) | 1461 | 2 | 5.665 | 0.042 |
| | | Error | 775 | 6 | | |

Table 3.4 Summary of ANCOVA for percentage chlorophyll *a* sloughed as a function of community type (four communities with two replicate substrata per community), with initial chlorophyll *a* concentration as the covariate. Overall adjusted $R^2$ for this analysis = 0.984.

| Source | S.S. | D.F. | F-ratio | P |
|---|---|---|---|---|
| Community | 1187 | 3 | 82 | 0.002 |
| Initial chlorophyll *a* | 85 | 1 | 18 | 0.025 |
| Error | 14 | 3 | | |

proportion sloughed, it is apparent that large differences in resistance to disturbance occurred among communities. Based on overall percentage biomass lost, a gradient in community resistance could be identified such that *Spirogyra* sp. $\leq$ *Melosira varians* < *Fragilaria construens* < *Fragiliaria vaucheriae*.

The relative response of individual taxa to the shear stress treatments varied within communities. Only the most abundant species are discussed here. While few specific comparisons were statistically significant (Table 3.5), some consistent trends were evident. The diatoms *Fragilaria vaucheriae* and *F. construens* either maintained or increased their relative abundances as a result of the shear stress treatment. This indicated, together with the biomass results, a high degree of resistance by *Fragilaria* to increases in shear stress. For the other abundant taxa the results were variable, but it was more common for there to be a decrease in relative abundance (*Cocconeis* sp. and *Gomphonema parvulum* were the notable exceptions). For the filamentous taxa, *Spirogyra* sp. and *Melosira varians* had large reductions in relative abundance (Table 3.5). In contrast, *Ulothrix zonata,* was more resistant, exhibiting increases in relative abundance with exposure of the communities to elevated shear stress.

Overall a high, and fairly similar, amount of chlorophyll *a* biomass persisted on the substrata after the highest shear stress treatment in all three diatom-dominated communities (20 - 30 $mg.m^{-2}$, Table 3.2). This biomass was composed of a uniform, basal, layer close to the substratum and was dominated by diatom species such as *Fragilaria vaucheriae, F. construens, Cymbella, minuta, Melosira varians* and *Gomphonema parvulum* (Table 3.5). This result indicates that even under very high shear stresses in streams it is possible for a significant periphyton community to persist (providing that no physical abrasion occurred).

*Kinetics of sloughing.*

Not only did I find significant differences in susceptibility of different communities to shear stress treatments, but their loss kinetics varied as well. This is important to quantify for understanding or predicting variable outcomes of low magnitude spates. The two non-filamentous, diatom-dominated communities had an approximately linear rate of biomass loss over the full range of shear stress treatments, the rate being higher for the *Fragilaria construens/Cymbella minuta/Achnanthidium minutissimum* community (Fig. 3.3). In contrast, both the filamentous communities displayed more asymptotic type loss kinetics. The *Melosira varians/Gomphonema parvulum* community was clearly the most fragile losing 23% of its chlorophyll *a* as soon as it was subjected to the lowest shear-stress treatment and a further two-fold loss as shear stress was increased from 1.2 to 3.0 $N.m^{-2}$ (i.e. by a factor of 3 above incubation shear velocity and equating to a mean water column velocity of 0.82 $m.s^{-1}$). After only an eight-fold increase in shear stress (1.10 $m.s^{-1}$ mean column velocity) the *Melosira varians/Gomphonema parvulum* community approached its maximum loss for the experiment (Fig. 3.3). Loss of chlorophyll *a* from the *Spirogyra* sp./*Gomphoneis herculeana/Ulothrix zonata* community occurred at a lower rate with low changes in velocity although 50% of the chlorophyll *a* was removed with only a six-fold increase in shear stress.

To compare the sensitivity of these communities to hydraulic shear, I determined the shear stress necessary for loss of 50% of chlorophyll *a*. This reflected the overall resistance of the communities to sloughing. A shear stress of 3.6 $N.m^{-2}$ was required for a 50% loss of the *Melosira varians/Gomphonema parvulum* community, 10 $N.m^{-2}$ for the *Spirogyra* sp./*Gomphoneis herculeana / Ulothrix zonata* community, 50.6 $N.m^{-2}$ for the *Fragilaria*

Table 3.5 Mean percentage abundance of common taxa in the four test communities before (initial) and following (after) the shear stress disturbance experiments (* P <0.05, † = P <0.01, for t-tests between initial and after percentage abundance).

| Community | Non-filamentous diatom communities | | | | Filamentous communities | | | |
|---|---|---|---|---|---|---|---|---|
| | A | | B | | C | | D | |
| | Initial | After | Initial | After | Initial | After | Initial | After |
| Chlorophyta | | | | | | | | |
| *Spirogyra* sp. | 2.5 | * 0.2 | 2.5 | 0.2 | 20.1 | * 2.1 | 0 | 0 |
| *Ulothrix zonata*(Weber & Mohr) Kütz | 1.9 | 2.3 | 1.9 | 2.3 | 14.5 | 53.3 | 0 | 0 |
| Bacillariophyta | | | | | | | | |
| *Achnanthidium lanceolata* (Breb.) Grun | 1.2 | 4.9 | 6.1 | 3.2 | 1.4 | 0.4 | 1.5 | 2.6 |
| *A. minutissima* Kütz | 3.8 | 6.9 | 10.0 | 4.9 | 0.3 | 0.5 | 0 | 0 |
| *Cocconeis* sp. | 3.1 | 5.5 | 1.8 | 2.5 | 7.6 | 10.6 | 0.3 | 0.5 |
| *Cymbella minuta* Hilse ex Rabh. | 24.1 | 18.5 | 11.4 | * 5.3 | 1.6 | 2.1 | 9.8 | 9.3 |
| *Fragilaria construens* (Ehr.) Grun | 0 | 0 | 25.7 | † 48.1 | 0 | 0 | 0 | 0 |
| *F. vaucheriae* (Kütz) Petersen | 24.2 | 26.1 | 5.9 | 11.1 | 2.3 | 2.4 | 1.6 | 3.0 |
| *Gomphoneis herculeana* (Ehr) Cleve | 10.6 | 9.3 | 1.2 | 1.3 | 17.5 | 12.1 | 1.3 | 0.5 |
| *Gomphonema parvulum* (Kütz) Grun | 0 | 0 | 0 | 0 | 0 | 0 | 14.8 | 27.4 |
| *Melosira varians* Ag | 0 | 0 | 0.8 | 0.2 | 2.9 | 2.0 | 49.9 | 26.1 |
| *Navicula avenacea* (Bréb). Cleve | 0 | 0 | 0 | 0 | 0 | 0 | 1.2 | 4.3 |
| *N. cryptocephala* Kütz | 0 | 0 | 5.6 | † 2.4 | 1.5 | 2.0 | 5.0 | 4.9 |
| *Nitzschia palea* (Kütz) W. Smith | 0.8 | 0.7 | 6.6 | * 2.4 | 12.9 | 2.2 | 1.8 | 2.1 |
| *Synedra ulna* (Nitzsch) Ehr | 13.4 | 4.7 | 0 | 0 | 4.8 | 2.5 | 0 | 0 |

*construens/Cymbella minuta/Achnanthidium minutissimum* community, and >90 $N.m^{-2}$ for the *Fragilaria vaucheriae/Cymbella minuta* community.

## IV. Discussion

Spates are important agents of natural disturbance in streams. During spates, sloughing and scouring of algal biomass by increases in shear stress and sediment abrasion can drastically affect periphyton (Fisher et al. 1982, Power and Stewart 1987). However, the present study has shown that a high variability in that response can potentially occur depending on the composition of the periphyton, as suggested previously from field studies (Chapter 2, see also Power and Stewart 1987, Grimm and Fisher 1989). This highlights the importance of considering degree of enrichment and associated community type, and not just the physical magnitude of the change in flow or shear stress (e.g. Biggs and Close 1989), in determining the likely effects of spates in streams.

I anticipated that at low shear stresses more periphyton would be sloughed from the substrata with longer exposure to the given treatment (i.e. resistance would decrease with duration of stress). This was based on the premise that with greater cumulative cell fatigue, structural failure would increase with time. However, for the *Melosira varians/Gomphonema parvulum* community used in the first experiment, there was an immediate loss of biomass with (generally) little further loss over time for all shear treatments suggesting that adhesion and inter-cellular connecting structures are not flexible (at least not for this community) and that critical shear stresses initiated sloughing. One significant negative coefficient occurred for percent change in chlorophyll *a* with duration of exposure to a shear stress of 5.3 $N.m^{-2}$ (Table 3.1). This could have been a result of slow re-deposition of sloughed material over time.

The highest forces would have occurred on those filaments that were observed to be occupying a zone up to 5 mm above the artificial substratum elements because of a) high form drag; b) the higher surface area of these filaments and, therefore, greater skin friction, and c) higher velocities above the substratum surface (Fig. 3.1). Indeed, observations during this experiment suggested that it was these "free-streaming" *Melosira varians* filaments that were lost first, during the low shear stress treatments, where even a 2-3 fold increase in shear stress

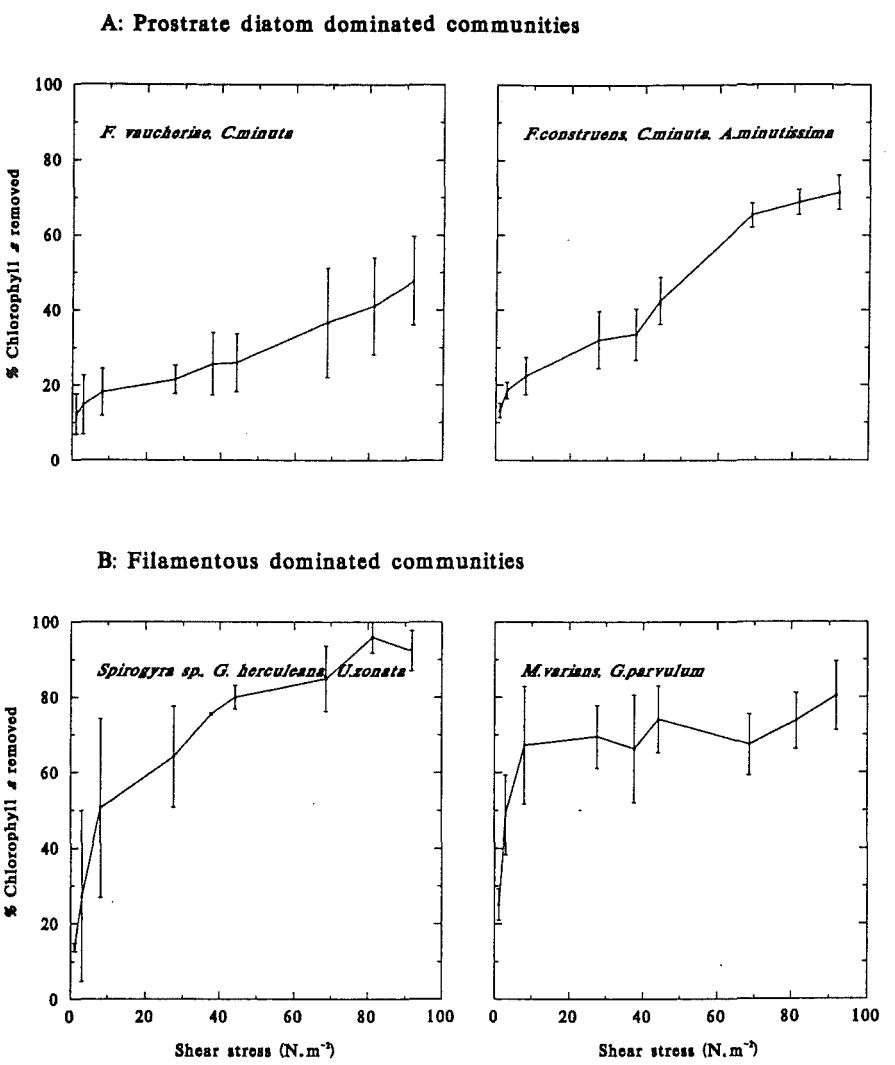


Fig. 3.3 Chlorophyll *a* removal kinetics as a function of experimental shear stress in four different periphyton communities. Error bars are one SE.

resulted in an 18-28% loss of chlorophyll *a*. Once this material was gone, the remaining community consisted of a more tightly bound basal layer of adnate diatoms such as *Gomphonema parvulum* which encased the substrata (see also results of community D in Table 3.5) . At the two highest shear stresses, this more tightly adhering mat started to disintegrate as well. This process occurred through small scale "plucking" rather than large scale peeling. Thus, if a communities' biomass is dominated by large filamentous algae, that have relatively high drag coefficients (Vogel 1981), then large amounts could potentially be removed with relatively low magnitude changes in shear stress. This supports field observations which indicate that *Melosira varians* mats are very fragile.

A strong difference in resistance to increases in shear stress was found between filamentous and low profile, non-filamentous, periphyton communities in the experiment analysing community differences in resistance. Furthermore, losses were not necessarily a linear function of disturbance intensity, as was also found by Biggs and Close (1989). For both filamentous communities tested, the first 50% of the biomass was removed at relatively low magnitude (<6 fold) increases in shear stress with asymptotic type kinetics, and in the case of the *Spirogyra* dominated community the underlying layers of basal cells were largely removed when stress exceeded a 30-fold increase. In contrast, the non-filamentous diatom-dominated communities were considerably more resistant, with <50% loss of biomass occurring even though shear stress was increased to >40 times the incubation shear stress. This indicates that streams that are dominated by weakly attached filamentous taxa (usually moderately enriched environments; Biggs and Price 1987) could be more susceptible to minor flow perturbations than streams dominated by non-filamentous diatoms (usually unenriched and/or heavily grazed environments; Biggs 1990, Biggs and Lowe 1994). Indeed, in my earlier work discussed in Chapter 2, I was unable to show a relationship between overall spate intensity and average biomass in low nutrient streams, but found a strong relationship for moderate and highly nutrient replete streams in New Zealand. In nutrient stressed/heavily grazed streams, spates causing entrainment of bed sediments are probably required before significant disturbance of periphyton occurs.

While the major difference in resistance was associated with growth form, there was also considerable variation in resistance within community types. The filamentous green alga *Spirogyra* experienced a 10-fold reduction in relative abundance, but *Ulothrix zonata* constituted 14.5% of the community prior to the shear stress treatment, and by the highest shear stress this taxon accounted for as much as 52.3%. This suggests that the attachment mechanisms of these two filamentous green algae differ markedly. *Ulothrix zonata* has specialized basal attachment cells that anchor the organism firmly to the substratum, and Poff et al. (1990) found that it had a high shear-stress resistance under steady-state flows. In contrast, *Spirogyra* is usually poorly attached or free-floating, but sometimes attached by lateral or terminal hapteroid outgrowths (Power and Stewart 1987). These form weaker connections than the holdfast of *Ulothrix zonata*. Among the non-filamentous diatom taxa there was also much variability. For example, *Nitzschia palea* did not appear to be well

attached, but taxa such as the apically attached *Fragilaria vaucheriae, Synedra ulna* and *Achnanthidium* spp. were. It is clear from this analysis that while the major differences in resistance were associated with differences in gross physiognomy of the communities, there were also more subtle differences in resistance among groups of taxa. Indeed Peterson et al. (1990) have shown greater removal of large chain forming *Fragiliaria*, solitary *Nitzschia* (many of which are only lightly silicified), and small, solitary *Navicula* by simulated wave action in a reservoir. *Navicula* and *Nitzschia*, in particular, possess relatively weak attachment abilities (Harper and Harper 1967), are often associated with particulate matter in the mat (rather than primary substratum), and are thus more easily removed from the periphyton (Peterson et al. 1990). In contrast, *Achnanthidium minutissimum* is widely reported to be highly resistant to disturbance (e.g. Peterson and Stevenson 1990). Thus, the overall resistance of a given taxon to increases in shear stress is a balance between drag (size and growth form), attachment strength, and tensile strength. While not specifically investigated here, a taxon's distribution within the mat will probably also influence susceptibility to disturbance.

The high resistance to elevations in shear stress of some non-filamentous diatom populations in this study reinforces the findings of field surveys in flowing waters (e.g. Luttenton and Rada 1986). This great resistance of many diatoms to water shear enables a remarkably high biomass of these species to persist on disturbed substrata. This gives these taxa a competitive advantage over groups such as green algae (Peterson and Stevenson 1990) and allows them to dominate high shear stress environments and/or streams with a high frequency of spates. Indeed, spate prone streams in New Zealand have communities that are commonly dominated by such taxa (i.e. *Fragilaria vaucheriae, Cymbella kappii, Cymbella minuta*), and also apically attached diatoms (e.g. *Gomphonema tenellum, Synedra ulna*) and the moderately shear resistant uniseriate filamentous green alga *Ulothrix zonata* (Biggs and Gerbeaux 1993, 1994). Thus, the high shear stress resistance of individual taxa probably has a very important influence on the longer-term species dynamics and competitive strategies of periphyton communities in streams.

This study has focused on "inherent" properties of periphyton communities which dictate their susceptibility to increases in shear stress. In doing this, I have linked different

gross physiognomies (filamentous vs. non-filamentous) with different resistance abilities, and also recognise much variation between taxa within these groups. However, for a given set of taxa, particular environmental conditions may modify these "inherent" properties and create an interaction between "inherent" and "conditional" factors. Reiter (1986) showed that communities that develop in different current, and/or resource regimes from the same seed population can be very similar taxonomically, but may differ considerably in mat physical structure. Similarly, I found (Chapter 5) that a *Cymbella/Gomphoneis/Synedra* dominated community formed thick mats high in mucilage content in high velocity riffles, but were thin (and loosely bound) in slow-flowing pools. The present results indicate that low magnitude spates could therefore have very different impacts on a given taxonomic assemblage of periphyton in pools and riffles where communities are physically different.

The all-pervading role of disturbance in ecology has led Grime (1979), among others, to adopt it as one of the primary axes of differentiation among vegetation assemblages, and in a number of recent reviews it has been suggested that disturbance (as a function of stream-flow variability) could provide a primary axis along which stream ecosystems are arrayed (e.g. Resh et al. 1988, Poff and Ward 1989, Fisher and Grimm 1991). Empirical studies that provide support for this view with respect to periphyton include Biggs (1988 and Chapter 2), Fisher and Grimm (1988), Biggs and Close (1989), Uehlinger (1991), and Lohman et al. (1992). The present study has demonstrated that flood-induced losses from different communities varies considerably and that a significant biomass of some taxa can persist through extreme events. This raises the fundamental questions as to "what degree of periphyton biomass loss actually constitutes a disturbance, and is the size of this loss predictable from stream flow data given the large number of factors affecting resistance?" Resolving such issues should be a priority for future research because they have important implications for the analysis and modelling of stream ecosystem dynamics.

## V. Summary

In Chapter 2, I found that there was a strong relationship between disturbance frequency/intensity and the mean monthly biomass of periphyton in moderate - highly enriched streams, but not in unenriched streams. The aim of this chapter was to investigated the cause

of this variable response with the possibility that it was due to differences in disturbance resistance of the communities dominating these environments. I hypothesised that large filamentous taxa, which generally dominate in moderate-highly enriched streams, should be more sensitive to flood disturbance than the low growing diatoms which dominate unenriched streams. The investigation was carried out experimentally using a laboratory flow tank and two communities dominated by adnate diatoms and two dominated by filamentous algae. The communities were subjected to nine different levels of shear stress ranging from 1 to 70-fold higher than the conditions to which the communities were acclimated. All communities were 14 days old, but some differences in initial biomass occurred which influenced the degree of resistance independently of species composition. Overall, the non-filamentous diatom communities typically found in unenriched streams were the most resistant, and the filamentous communities were the least resistant. The kinetics of the sloughing process varied among community types, with a community dominated by *Melosira varians/ Gomphonema parvulum* losing 50% of its biomass with only a 3 fold increase in shear stress. In contrast, a community dominated by the non-filamentous diatoms *Fragilaria vaucheriae* and *Cymbella minuta* lost <50% of its biomass after a seventy fold increase in shear stress. Shear stresses required for 50% loss of biomass for the different communities were as follows: 3.6 Newtons.m$^{-2}$ for the *Melosira varians/Gomphonema parvulum* community; 10.0 N.m$^{-2}$ for the *Spirogyra* sp./*Gomphoneis herculeana/Ulothrix zonata* community; 50.6 N.m$^{-2}$ for the *Fragilaria construens/Cymbella minuta/Achnanthes minutissima* community, and >90.0 N.m$^{-2}$ for the *Fragilaria vaucheriae/Cymbella minuta* community. These results show that spates without bedload movement can potentially have widely differing disturbance effects on periphyton loss among streams depending on the initial taxonomic composition of resident communities. These results have important implications for stream ecosystem analysis and modelling among streams which vary in enrichment.

## VI. References

Biggs, B. J. F. 1988. Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verh. Internat. Verein. Limnol.* 23:1405-11.

Biggs, B. J. 1990. Periphyton communities and their environments in New Zealand rivers. *N.Z. J. Mar. Freshw. Res.* 24:367-86.

Biggs, B. J. F. & Close, M. E. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biol.* 22:209-31.

Biggs, B. J. F., Duncan, M. J., Jowett, I. G., Quinn, J. M., Hickey, C. W., Davies-Colley, R. J. & Close, M. E. 1990. Ecological characterisation, classification and modelling of New Zealand rivers: an introduction and synthesis. *N.Z. J. Mar. Freshw. Res.* 24:277-304.

Biggs, B. J. F. & Gerbeaux, P. 1993. Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. *N.Z. J. Mar. Freshw. Res.* 27:39-53.

Biggs, B. J. F. & Gerbeaux, P. J. 1994. Epilithic periphyton in temperate rivers: community composition in relation to differences in disturbance regimes. *NIWA-Christchurch Miscellaneous Report* 177:33p.

Biggs, B. J. F. & Hickey, C. W. 1994. Periphyton responses to a hydraulic gradient in a regulated river, New Zealand. *Freshwater Biol.* 32:49-59.

Biggs, B. J. F. & Lowe, R. L. 1994. Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *N.Z. J. Mar. Freshw. Res.* 28:119-34.

Biggs, B. J. F. & Price, G. M. 1987. A survey of filamentous algal proliferations in New Zealand rivers. *N.Z. J. Mar. Freshw. Res.* 21:175-91.

Fisher, S. G., Gray, L. J., Grimm, N. B. & Busch, D. E. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecol. Monogr.* 52:93-110.

Fisher, S. G. & Grimm, N. B. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verh. Internat. Verein. Limnol.* 23:1183-90.

Fisher, S. G. & Grimm, N. B. 1991. Streams and disturbance: are cross-ecosystem comparisons useful? *In* J. Cole, G. Lovett & S. Findlay *Comparative analyses of ecosystems-patterns, mechanisms and theories.* Springer-Verlag, New York, .

Gordon, N. D., McMahon, T. A. & Finlayson, B. L. 1992. *Stream Hydrology: an introduction for ecologists.* John Wiley & Sons, Brisbane, .

Grime, J. P. 1979. *Plant Strategies and Vegetation Processes.* John Wiley and Sons.

Grimm, N. B. & Fisher, S. G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *J. North Am. Benthol. Soc.* 8:292-307.

Harper, M. A. & Harper, J. F. 1967. Measurements of diatom adhesion and their relationship with movement. *Br. Phycol. Bull.* 3:195-207.

Hicks, D. M. & Mason, P. D. 1991. *Roughness characteristics of New Zealand rivers.* DSIR Marine and Freshwater, Wellington, NZ.

Horner, R. R., Welch, E. B., Seeley, M. R. & Jacoby, J. M. 1990. Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biol.* 24:215-32.

Koehl, M. A. R. 1982. The interaction of moving water and sessile organisms. *Sci. Am.* 247:124-34.

LaCoursiere, J. O. & Craig, D. A. 1990. A small flume for studying the influence of hydrodynamic factors on benthic invertebrate behaviour. *J. North Am. Benthol. Soc.* 9:358-67.

Lohman, K., Jones, J. R. & Perkins, B. D. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Can. J. Fish. Aquat. Sci.* 49:1198-205.

Luttenton, M. R. & Rada, R. G. 1986. Effects of disturbance on epiphytic community architecture. *J. Phycol.* 22:320-26.

Peterson, C. G., Hoagland, K. D. & Stevenson, R. J. 1990. Timing of wave disturbance and the resistance and recovery of a freshwater epilithic microalgal community. *J. North Am. Benthol. Soc.* 9:54-67.

Peterson, C. G. & Stevenson, R. J. 1990. Post-spate development of epilithic algal communities in different current environments. *Can. J. Bot.* 68:2092-102.

Peterson, E. G. & Stevenson, R. J. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73:1445-61.

Poff, N. L., Voelz, N. J. & Ward, J. V. 1990. Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *J. North Am. Benthol. Soc.* 9:303-18.

Poff, N. L. & Ward, J. V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.* 46:1805-18.

Power, M. E. 1992. Hydrological and trophic controls of seasonal algal blooms in northern California rivers. *Arch. Hydrobiol.* 125:375-410.

Power, M. E. & Stewart, A. J. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 117:333-45.

Reiter, M. A. 1986. Interactions between the hydrodynamics of flowing water and the development of a benthic algal community. *Journal of Freshwater Ecology* 3:511-17.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Hiram, W. L., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, J. B. & Wissmar, R. C. 1988. The role of disturbance instream ecology. *J. North Am. Benthol. Soc.* 7:433-55.

Robinson, C. T. & Rushforth, S. R. 1987. Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiol.* 154:49-59.

Rounick, J. S. & Gregory, S. V. 1981. Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. *Hydrobiol.* 83:197-205.

Sartory, D. P. & Grobelaar, J. E. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiol.* 114:177-87.

Smith, D. G. & Maasdam, R. 1994. New Zealand's National River Water Quality Network. 1. Design and physico-chemical characterisation. *N.Z. J. Mar. Freshw. Res.* 28:19-35.

Steinman, A. D., Mulholland, P. J., Palumbo, A. V., Flum, T. F., Elwood, J. W. & DeAngelis, D. L. 1990. Resistance of lotic ecosystems to a light elimination disturbance: a laboratory stream study. *Oikos* 58:80-90.

Tett, P., Gallegos, C., Kelly, M. G., Hornberger, G. M. & Cosby, B. J. 1978. Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. *Limnol. Oceanogr.* 23:785-97.

Uehlinger, U. 1991. Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Arch. Hydrobiol.* 123:219-37.

Vogel, S. 1981. *Life in Moving Fluids.* Princeton University Press, Princeton.

# Chapter 4

## Periphyton Resilience Following Flood Disturbance: the influence of spatial differences in post-flood hydraulic habitat conditions

**Preface**

In the previous chapter I analysed the susceptibility (and thus resistance) of different periphyton communities to flood disturbance. In the following chapter, I analyse the recovery of communities from such events. Sites in two rivers were sampled for 60 - 110 days following floods, at weekly or bi-weekly intervals. Water velocities immediately above the substrata were also measured. There were no new flood events within the sampling time for one of the sites, but a flood after 50 days removed most of the accumulated biomass in the second river. My objective was to determine how long it can take for periphyton biomass redevelopment, the kinetics of this process, and how it varies spatially as a function of post-disturbance water velocity. This aspect of my study addresses issues of hydraulic disturbance, hydraulic habitat requirements of periphyton and the influence of near-bed hydraulics on growth and loss processes in a field setting. This manuscript has been published in *Regulated Rivers: Research and Management* **12:** 251-261.

## I. Introduction

Relatively minor changes in velocity can result in major changes in near-bed physics which can have a significant influence on periphyton accrual in rivers (see Stevenson 1996). Such velocity changes can be particulary important as communities attempt to regenerate following flood disturbance. However, the functional significance of velocity appears to vary depending on the age of the community and the dominant growth process occurring at the time. Often the effects of velocity may be counter-acting. For example, as an algal mat regenerates following a disturbance, spatial or temporal changes in velocity can influence the thickness of the laminar boundary layer close to the mat which, in-turn, alters diffusion resistance for essential elements. This can result in enhanced periphytic metabolic rates (e.g., Whitford and Schumacher 1961, Lock and John 1979). However, changing velocities can also have a major effect on shear stress, which increases at a rate proportional to the square of the shear velocity. This can greatly alter drag on the communities (particularly as they grow up into the `free stream' above the substrata) and the potential for cell dislodgement (Stevenson 1983, Stevenson and Peterson 1989, Biggs Chapter 3). Thus, early in the accrual cycle it is likely that high velocities will inhibit the settlement of propagules and late in the cycle they could inhibit development of high biomass.

Despite the importance of hydraulic conditions following floods to periphyton in rivers, very little is known about the interactive effects of time since disturbance and water velocity on regeneration dynamics in natural sreams. Based on previous experimental studies (see Stevenson 1996, for a review), it may be hypothesised that immigration and community establishment should be favoured by low velocity; exponential growth should be favoured by medium and high velocities; and late accrual phase biomass should be favoured by intermediate velocities where higher mass transfer can maintain high levels of production, but shear stress is not severe. Ultimately, if flows are stable for long enough, and the periphyton biomass has passsed its peak, community growth and loss processes should reach an equilibrium. If nutrient concentrations are high enough at such times (counteracting the lower mass transfer under lower velocities) a strong negative relationship between biomass and water velocity should develop.

The specific objective of the present study was to investigate the effects of spatial differences in water velocity on periphyton colonisation and growth rates following catastrophic disturbance. It was carried out in two rivers (New Zealand and Norway) using natural substrates following flood events which reset community development to near zero biomass.

## II. Study Areas

*Okuku River, Canterbury, New Zealand*

The Okuku River had its headwaters in the foothills of the Southern Alps, New Zealand, at an altitude of 800 - 1,200 m. The dominant rock type was nutrient poor metamorphosed fine-grained sandstone, and landuse in the catchment was low intensity pastoral farming. Vegetation cover was subalpine tussock grass and scrub at higher altitudes, and beech forest (*Nothofagus* spp.) at mid-altitudes. In the lower catchment there was more intensive pastoral agriculture on the terraces adjacent to the stream channel. Riparian vegetation was predominantly crack willow (*Salix fragilis*). However, because the flood channel was usually several hundred meters wide this vegetation rarely shaded the active, meandering stream channel. The average slope of the river was approximately 1/200. The bed of the channel was composed of cobbles and boulders in riffles, grading to cobbles and gravels in runs, and gravels and coarse sand in pools.

*River Sokna, Trøndelag, Norway*

River Sokna was located in central Norway, and had a catchment of 549 $km^2$. Mean altitude of the catchment is 600 m above sea level and mean annual discharge is 12.4 $m^3s^{-1}$. Bedrock was nutrient poor and the intensity of agriculture was very low in the area.

The river bed was stable with an armoured layer of cobbles and boulders limiting both erosion and the meandering of the river. The slope of the river was about 1/50. At the top of the armoured layer mass transport of sand and cobbles was apparent during flood events. Floods occur frequently throughout the year except in winter when the catchment is snow-covered and the river is partly ice-covered. The annual maximum flood was about 200 $m^3 s^{-1}$.

## III. Sampling Strategy

*Okuku River, New Zealand*

Four sampling sites were selected in the lower catchment, the sites being 2-4 km apart. In early spring a large flood throughout the catchment (> 20 times the preceding baseflow) resulted in major bed sediment movement and re-arrangement of the channel at all sites. Flows decreased fairly slowly after the flood, but after 14 days the water had returned to baseflow clarity and a normal riffle, run, pool structure had re-developed. Little periphyton growth was evident at the sites until 30 days after the flood peak; sampling commenced at bi-weekly intervals 35 days (Day 35) after the flood peak (Day 0), except for Site 1 when sampling commenced on Day 49.

*River Sokna, Norway*

One site in the river consisting of both a pool and a riffle, was chosen for sampling. The site was located near a discharge gauging station, and consisted of four fixed transects marked with poles on each of the river banks. A marked wire was stretched between the poles to define fixed sampling points in the river where sampling was undertaken weekly. Sampling started just after a major flood in summer and was terminated just after the next flood occurred.

## IV. Methods

*Field Procedures: Okuku River, New Zealand*

On each sampling occasion, points covering a range of velocities (0.1 - 0.8 m $s^{-1}$), within a fairly narrow depth range (0.2 - 0.4 m), were identified at each site using a Gurley current meter and wading rod. Depth and near-bed velocity (5cm from the bottom) were recorded at each point, and the stone immediately beneath retrieved for sampling of periphyton. Five points were sampled at most sites during the colonisation phase and this was increased to 10 samples during exponential growth of the mats. An extra sampling was also carried during exponential growth (Day 71) to more accurately define the regeneration dynamics during this period of rapid change in biomass.

The stone from each sampling point was returned to the river bank and a circle of a known diameter (which varied depending on the stone size) was scribed on the top surface. All material, including a small amount of rock slithers, were then removed from within this area using a

scalpel. All stones were fine-grained, hard and worn smooth by sediment transport processes. The gross colour and character of the community on each stone were noted, and the general quantity and type of invertebrates in the mat recorded. Periphyton samples were then placed in individual polyethylene containers with river water and chilled for transport to the laboratory.

Triplicate water samples were collected for nutrient analysis in a 60ml syringe from mid-stream at the completion of the periphyton sampling and filtered using a Swinex portable filtering apparatus and 0.45 micron pore size cellulose acetate filters. Each filter was pre-rinsed with 95% methanol followed by stream water. The filtrate (generally 60ml) for each replicate was returned to the laboratory on ice.

*Field Procedures: River Sokna, Norway*

On each sampling occasion, a total of 38 fixed points on the 4 transects were photographed with an underwater camera placed in a frame giving a sampling area of 30 x 40 cm (e.g., Rørslett et. al. 1978, Rørslett et. al. 1989). This allowed replicated sampling to be undertaken at exactly the same point without disturbing the periphyton community and regardless of substratum size.

For each photograph the thickness of the mat in categories of 1 (thin) to 3 (thick), and percentage cover, were estimated using a stereo-microscope at 40x magnification. These estimates were then converted to estimates of ash-free dry mass (AFDM) biomass based on a previous calibration of the thickness categories with AFDM (Stokseth 1994). Biomass values were multiplied the by the proportional cover in each category.

The mean water column velocity (0.4 x depth above the substrata), nearbed velocity (5cm above the bed) and depth were measured at all fixed points. Velocities were measured twice at different low water discharges using an Ott current meter and a wading rod. The average velocities for each sampling point over the accrual cycle were then calculated by hydraulic modelling (Stokseth 1994). Maximum and minimum discharges during the period were 15.0 $m^3 s^{-1}$ and 4.0 $m^3 s^{-1}$, respectively.

*Laboratory Procedures*

Each periphyton sample from the Okuku River was collected onto a pre-ashed, Whatman, GFC filter and macroinvertebrates were removed with forceps. Samples were dried at 105°C for 24 hours, cooled in a desiccator and weighed. They were then ashed at 400°C for 4 hours before cooling and re-weighing. The difference between dry and ash weights (AFDM) is used as a measure of total periphyton biomass. Nutrient concentrations in the Okuku River were measured on a Technicon 2 autoanalyser. Dissolved reactive-P was determined using the molybdate method with ascorbic acid reduction (APHA 1985); ammonia-N was determined with the indophenol blue method (APHA 1985); and nitrate-N by hydrazine reduction followed by colorimetric determination (Kamphake et al., 1967). Nitrate-N and ammonia-N data are combined for each sample to give total inorganic-N.

Water samples were collected four times from the River Sokna and analysed for total-P according to the Norwegian Standard method (NZ 4725). Water temperatures were measured at the site.

*Data Analysis*

Data analyses were carried out using SYSTAT (Wilkinson 1990) for the Okuku River data and SPSS (Norusis/SPSS 1992) for the River Sokna. The non-parametric Kruskal-Wallis one-way analysis of variance was used to determine among-site differences in periphyton biomass for different stages of accrual. A similar analysis was carried out for the data pooled across all sites, but divided into velocity groups, for each stage of accrual. Finally, scatter plots of AFDM as a function of velocity and depth were drawn for each stage of accrual with trends to define habitat suitability being defined using a locally weighted average smoothing line (SMOOTH = LOWESS).

Log-linear regression was used for estimating the exponential growth rate according to the following model:

$$y = a \exp(kt)$$

where y is the AFDM concentration (g $m^{-2}$) at day $t$, a is the initial chlorophyll $a$ concentration at $t = 0$, and $k$ is the net growth rate.

## V. Results

*General*

Table 4.1 summarises average hydraulic, nutrient and periphyton AFDM data for all the sites.

The two rivers were slightly different, the most clear hydraulic differences being that the Norwegian river was deeper and steeper than the New Zealand river. This indicates that the average shear stress in River Sokna should be about 10 times the average shear stress in the Okuku River. Mean water column velocities were not measured in the New Zealand river, but the mean velocities at the sampling points in the two rivers were within the same range since the New Zealand river was very shallow and velocity measurements 5cm above the substratum were therefore reasonably close to the velocity at 0.4 of the depth. The ranges of near bed velocities were higher in the New Zealand river which had finer substrata and therefore was likely to be less stable than the Sokna.

Total phosphorus concentration was moderate in the Norwegian River, averaging 26.5 ug $l^{-1}$. At the New Zealand sites average concentrations of dissolved reactive-P, and total inorganic-N, were also moderate (Table 4.1). The N:P ratio for the average concentrations at each site were generally <5 suggesting that nitrogen was in relatively short supply compared with phosphorus, and thus that nutrient mass transfer was potentially limiting rates of cell division during the accrual cycle.

Average AFDM was moderate to low over the accrual cycle at all sites in both rivers (c.f., Biggs and Price 1987). In the Okuku, significant ($P < 0.05$) difference in AFDM among the sites was found on only one of the six sampling occasions (Day 71, Table 4.2). Thus, for the remainder of the analysis data from the four Okuku sites were pooled.

Table 4.1: Summary of average hydraulic, nutrient and periphyton data for the different sampling sites in the Okuku River, New Zealand and the River Sokna, Norway. The duration of the post-spate sampling period was 100 days for the Okuku and 64 days for the Sokna.

| Variable | Okuku, Site 1 | Okuku, Site 2 | Okuku, Site 3 | Okuku, Site 4 | Sokna site |
|---|---|---|---|---|---|
| N | 45 | 50 | 50 | 70 | 266/38* |
| Av. nearbed velocity (m $s^{-1}$) (S.D.) | 0.39 (0.20) | 0.53 (0.23) | 0.55 (0.27) | 0.51 (0.23) | 0.26 (0.145) |
| Av. column velocity (m $s^{-1}$) (S.D.) | - | - | - | - | 0.48 (0.17) |
| Av. depth (m) (S.D.) | 0.27 (0.09) | 0.23 (0.07) | 0.26 (0.09) | 0.23 (0.07) | 0.71 (0.17) |
| Av. slope | 1/200 | 1/200 | 1/200 | 1/200 | 1/50 |
| Av. shear stress $t_0$ (N $m^{-2}$) $t^0$=rg*Depth *Slope | 13.2 | 11.3 | 12.8 | 11.3 | 139.3 |
| Gravel (%) d=2-20mm | 0 | 20 | 40 | 10 | 5 |
| Cobble (%) d=20-200mm | 60 | 60 | 60 | 50 | 35 |
| Boulder (%) d >200mm | 40 | 40 | 20 | 10 | 60 |

Table 4.1 Cont.

| | | | | | |
|---|---|---|---|---|---|
| Av. dissolved reactive-P (mg $l^{-1}$) (S.D.) | 3.3 (0.84) | 5.6 (0.93) | 5.4 (0.67) | 3.5 (1.73) | - |
| Av. total inorganic-N (mg $l^{-1}$) (S.D.) | 15.3 (10.5) | 23.2 (10.2) | 22.4 (9.9) | 22.8 (9.4) | - |
| Av. total P (mg $l^{-1}$) (S.D.) | - | | | | 26.5 (6.6) |
| Av. water temp. (°C) | 16.6 | 16.6 | 16.6 | 16.6 | 7.5 |
| Av. AFDM (g $m^{-1}$) (S.D.) | 15.1 (16.7) | 16.9 (17.0) | 12.7 (12.4) | 22.0 (21.2) | 5.8 (6.5) |

(*38 fixed points and a total of 266 periphyton samples.)

Table 4.2: Non-parametric analysis of variance of periphyton AFDM at different stages of accrual among the four sampling sites, Okuku River, New Zealand.

| Days of accrual | Kruskal-Wallis statistic | N | Probability |
|---|---|---|---|
| 35 | 1.943 | 15 | N.S. |
| 49 | 5.873 | 20 | N.S. |
| 63 | 7.477 | 40 | N.S. |
| 71 | 12.206 | 40 | <0.01 |
| 77 | 4.026 | 40 | N.S. |
| 92 | 6.808 | 40 | N.S. |

*Effects of Nearbed Velocities On Colonisation, Growth and Peak Biomass of Periphyton; Okuku River New Zealand:*

Periphyton colonisation (defined here as the initial section of linear kinetics on the accrual curve) took approximately 50 days (Fig. 4.1). Exponential accrual of the mat then occurred. Over the following 30 days, AFDM increased almost 7 fold with average peak biomass for the sites being 27 g $m^{-2}$. Autogenic sloughing then commenced as the communities started to degrade. As the periphyton community matured, dominance was observed to change from diatoms to a combination of diatoms and green filamentous algae (*Spirogyra* sp. and *Oedogonium* sp.).

Benthic invertebrates were rare following the flood, however, by Day 49 chironomid and blackfly larvae were commonly observed on stones. A greater diversity of invertebrates became increasingly abundant during the period of accrual, with mobile and attached cased caddis larvae becoming prominent (and dominant on many stones) by Day 71. When sloughing commenced (> Day 77), very high densities of insects occurred within the matrix. These communities were dominated by chironomid larvae, with caddis larvae being abundant. With sloughing the invertebrates inhabiting the matrix were all exported downstream with the periphyton community, leaving an invertebrate assemblage dominated by cased caddis larvae and many mayflies on the undersides of the stones.

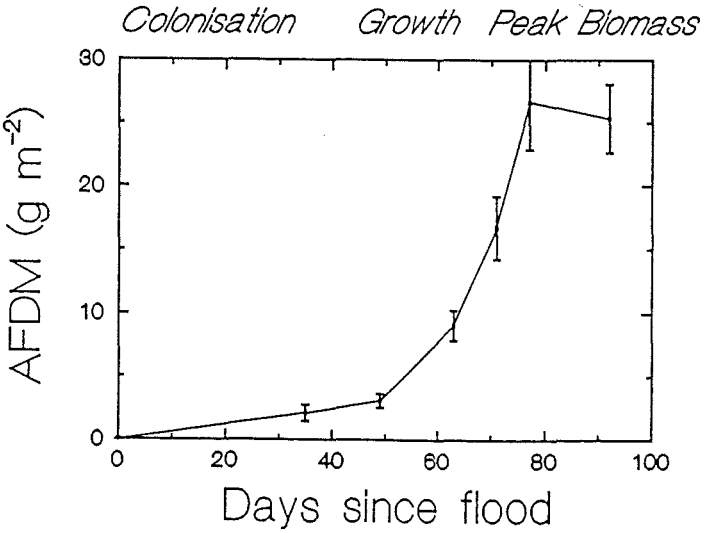


Figure 4.1: Accrual curve for the Okuku River periphyton (AFDM) following a flood. Error bars are standard errors.

*a) Accrual Dynamics at Different Velocities*

The periphyton data were arbitrarily split into three different groups for each sampling occasion based on their associated nearbed velocities: low, <0.3 m $s^{-1}$; medium, 0.3 - 0.7 m $s^{-1}$; and high > 0.7 m $s^{-1}$. Little difference in biomass occurred between these groups during initial colonisation (Fig. 4.2). However, at the beginning of the exponential growth phase, greater development occurred under low velocities, although the differences in AFDM were not statistically significant (Table 4.3). By Day 63 biomass in all velocity groups merged again as that of for the medium and high velocity communities caught, and then passed that of the low velocity communities. The high velocity communities then grew very fast and peak biomass was observed on Day 77, when the low velocity community was starting to slough. At this point there was a significant (i.e., $P < 0.05$, Table 4.3) difference in AFDM among the communities. The high velocity communities began to slough after Day 77, whereas those growing at medium velocities continued to accrue, but at a lesser rate (Fig. 4.2). By Day 92 the medium velocity communities had the greatest biomass and differences among groups were still significant. Following Day 92, autogenic sloughing occurred in the medium and high velocity ranges leaving large areas of clean streambed. Sampling was curtailed at this point.

Table 4.3: Non-parametric analyses of variance of periphyton AFDM at different stages of accrual among the three nearbed velocity groups (Low: v <0.3 m $s^{-1}$, Medium: v = 0.3 m $s^{-1}$ -0.7 m $s^{-1}$, High: v >0.7 m $s^{-1}$) in the Okuku River, New Zealand.

| Days of accrual | N in velocity-group LOW | N in velocity-group MEDIUM | N in velocity-group HIGH | Kruskal-Wallis statistic | Probability |
|---|---|---|---|---|---|
| 35 | - | 11 | 4 | 24.00(*) | N.S. |
| 49 | - | 7 | 13 | 26.50(*) | N.S. |
| 63 | 11 | 25 | 4 | 1.433 | N.S. |
| 71 | 11 | 23 | 6 | 0.654 | N.S. |
| 77 | 7 | 27 | 6 | 8.594 | <0.05 |
| 92 | 12 | 22 | 6 | 6.929 | <0.05 |

(*) Kruskal-Wallis statistics were replaced by Mann-Whitney U statistics because data were only available for two velocity groups.

Net community growth rates (Table 4.4) were highest at low velocities during the colonisation phase, and lowest at high velocities. However, following this phase (i.e., Days 63-77), growth of the low velocity community ceased, whereas the growth rate of the high velocity community was 50% higher than at medium velocity.

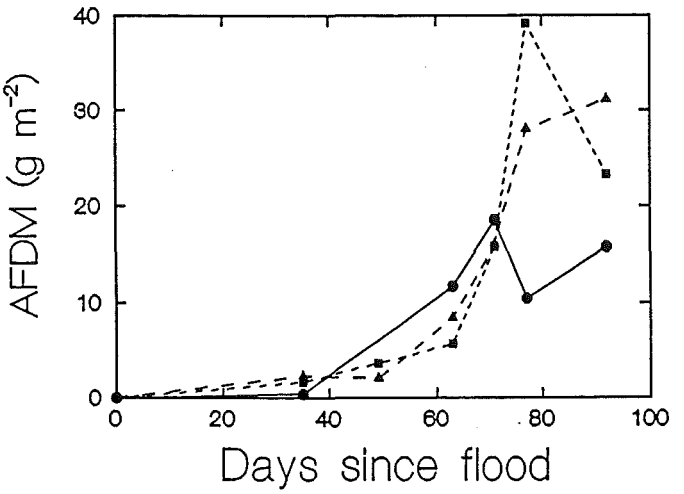


Figure 4.2: Periphyton AFDM accrual in the Okuku River at low (< 0.3 m $s^{-1}$, dots) medium (0.3 - 0.7 m $s^{-1}$, triangles) and high (> 0.7 m $s^{-1}$, squares) velocities.

*b) Velocity Suitability for Different Stages of Accrual*

There was little difference in community biomass as a function of velocity during early colonisation in the Okuku River (Fig. 4.3). However, by Day 71 areas of low velocity (i.e., <0.3 m $s^{-1}$) had the highest biomass. Over a 6 day interval, however, this relationship was completely reversed due to sloughing in the low velocity areas and high growth rates at high velocities. The relationship of biomass with velocity continued to be dynamic as the community aged, and by the time of community maturity (Day 92), a unimodal distribution of biomass had developed with a peak in AFDM at 0.5 - 0.7 m $s^{-1}$.

Table 4.4: Summary of periphyton community growth rates (k) during periods of colonization and exponential growth for the three velocity groups in the two different rivers. Note that the Okuku River data were grouped according to different nearbed velocities, whereas the River Sokna data were grouped according to different mean water column velocities.

| Velocity groups | Period of colonisation, Okuku River (0-63 days) | Period of exponential growth, Okuku River (63-77 days) | Period of colonisation, River Sokna (0-17 days) | Period of exponential growth River Sokna (17-44 days) |
|---|---|---|---|---|
| Growth rate of mat at low velocity (<0.3 m $s^{-1}$) ($g\ m^{-2}\ d^{-1}$) | 0.039 | -0.004 | 0.076 | 0.069 |
| Growth rate of mat at medium velocity (0.3-0.7 m $s^{-1}$) ($g\ m^{-2}\ d^{-1}$) | 0.032 | 0.080 | 0.031 | 0.063 |
| Growth rate of mat at high velocity (>0.7 m $s^{-1}$) ($g\ m^{-2}\ d^{-1}$) | 0.031 | 0.128 | 0.017 | 0.062 |

*River Sokna, Norway:*

Periphyton colonization took about 10-20 days after the flood peak (134 $m^3\ s^{-1}$), at which time exponential growth of the mat began (Fig. 4.4). Biomass increased to an average of 15.2 $g\ m^{-2}$ after 45 days. Dominant taxa were the diatom *Didymosphenia geminata* and the green filamentous alga *Ulothrix zonata.* Benthic invertebrates were rarely observed during the sampling period. A second flood of 120 $m^3 s^{-1}$ occurred on Day 49 before the communities in any of the velocity-groups had reached their probable peak biomass.

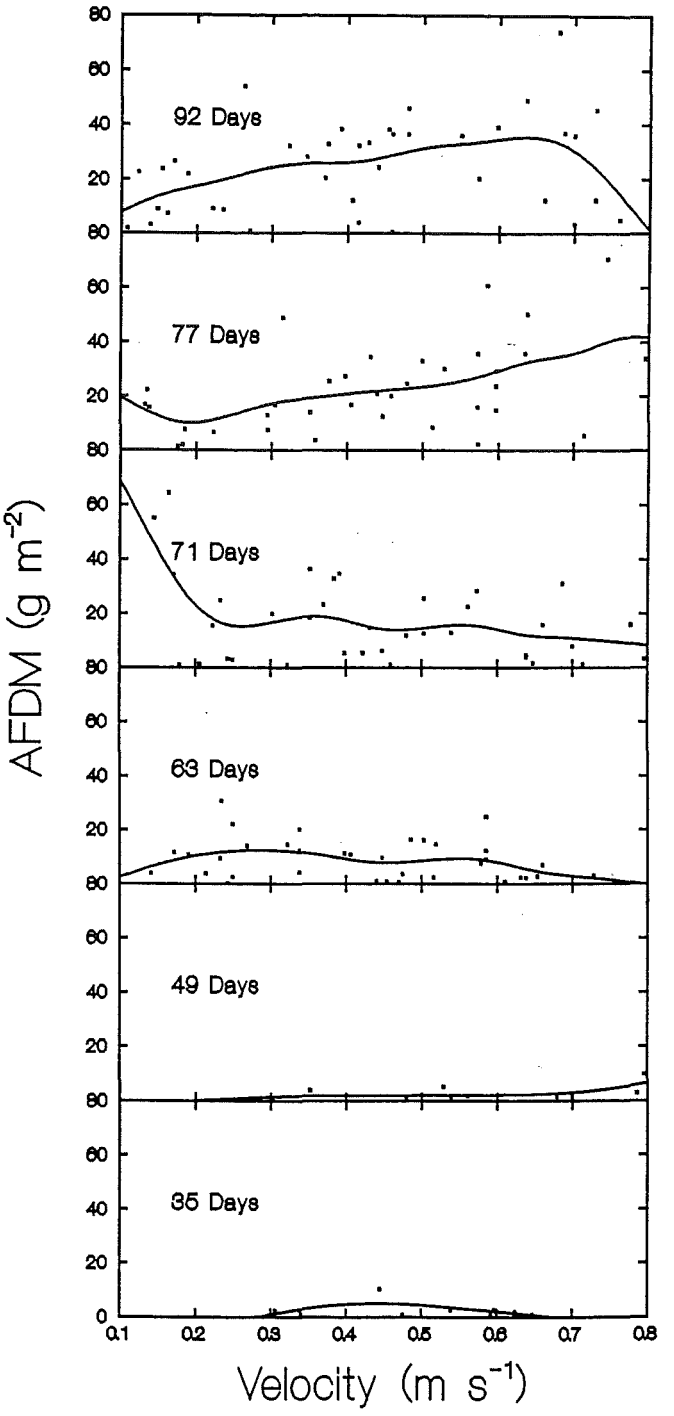


Figure 4.3: Periphyton AFDM as a function of velocity for different stages of accrual in the Okuku River. The best-fit lines were generated by a locally weighted smoothing technique (Wilkinson 1990).

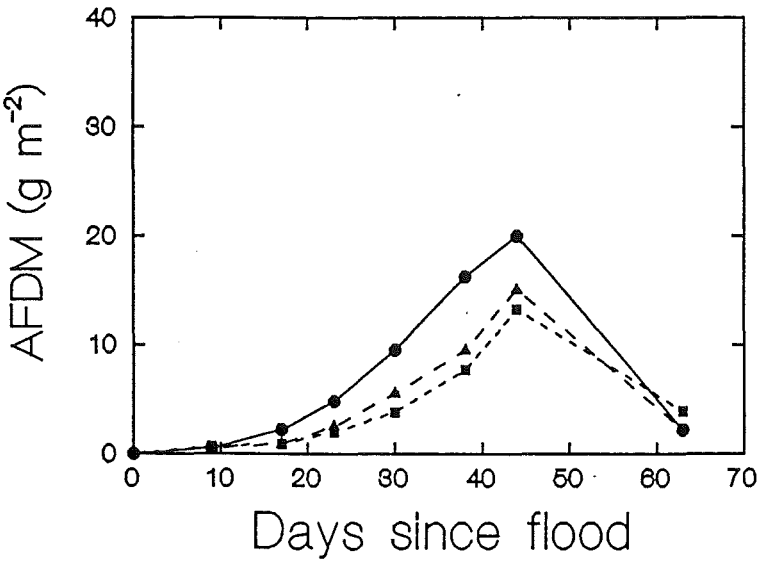


Figure 4.4: Periphyton AFDM accrual in the River Sokna at low (< 0.3 m $s^{-1}$, dots), medium (0.3 - 0.7 m $s^{-1}$, triangles) and high (> 0.7 m $s^{-1}$, squares) velocities.

*a) Accrual Dynamics at Different Velocities*

The periphyton data were split into three different groups based on the mean water column velocity of each sample. No significant differences in biomass were found between the groups 9 days after the flood (Table 4.5, Fig. 4.4). After the period of colonization differences between the groups became significant ($P < 0.05$), however, with biomass being higher in low-velocity areas. By Day 44 there was again no significant difference in biomass between the groups. On Day 49 a second flood occurred and biomass fell drastically.

Growth rate of the periphyton community was highest during initial colonisation under low velocities (as in the Okuku River), but there was little difference in growth rates of the velocity groups during the exponential phase of the accrual cycle (Table 4.4).

Table 4.5: Non-parametric analysis of variance of periphyton AFDM at different stages of accrual among the three mean column velocity groups (Low: v <0.3 m $s^{-1}$, Medium: v = 0.3 m $s^{-1}$ - 0.7 m $s^{-1}$, High: v >0.7 m $s^{-1}$) in the River Sokna, Norway.

| Days of accrual | N in velocity-group LOW | N in velocity-group MEDIUM | N in velocity-group HIGH | Kruskal-Wallis statistic | Probability |
|---|---|---|---|---|---|
| 9 | 6 | 21 | 11 | 1.347 | N.S. |
| 17 | 6 | 21 | 11 | 4.215 | N.S. |
| 23 | 6 | 21 | 11 | 6.924 | <0.05 |
| 30 | 6 | 21 | 11 | 7.102 | <0.05 |
| 38 | 6 | 21 | 11 | 7.098 | <0.05 |
| 44 | 6 | 21 | 11 | 1.304 | N.S. |
| 63 | 6 | 21 | 11 | 3.930 | N.S. |

## VI. Discussion

The higher rate of colonisation in the low velocity communities in both rivers most likely reflected differences in propagule attachment as a function of velocity. AFDM is not sensitive enough to show differences in immigration, but the benefits of low velocities for propagule establishment have been clearly defined experimentally (e.g., Stevenson 1983). Conversely, the more rapid development of the medium and high velocity communities during the growth phase in the Okuku River was probably due to enhanced nutrient transfer. More rapid growth under higher velocities has also been demonstrated by McIntire (1966) in a laboratory flume. However, until now this has not been demonstrated in the field under natural conditions following stream disturbance.

Horner and Welch (1981) found that the optimum velocity (i.e., where mass transfer is enhanced, but shear stress is not excessive) for mature periphyton communities on artificial substrata in unenriched streams was about 0.5 m $s^{-1}$. Further, in laboratory flumes Horner et al. (1990) found maximum biomass at 0.6 m $s^{-1}$ at a DRP concentration of 7.5 mg $l^{-1}$. The Okuku results are in agreement with these figures, with maximum biomass as a function of velocity occurring at the peak of the growth cycle (Day 92, Fig. 4.1) at between 0.5 and 0.7 m $s^{-1}$ (Fig. 4.3).

The low velocity community in the Okuku sloughed earliest in the accrual cycle (Fig. 4.2). Under low velocities and low free-stream nutrient concentrations, the overstory of a mat can potentially limit the supply of nutrients to the understory (Stevenson and Glover 1993). Such a process could then lead to degradation of the underlayers and detachment. However, the high velocity communities commenced sloughing soon after this as well. For these communities though, biomass was twice that of the low velocity communities and high enough to be classified as a proliferation (i.e., 40 g $m^{-1}$ AFDM; Biggs and Price 1987). It is likely that the sloughing of these high velocity communities was more a function of the drag being induced by the height of the mat exceeding the attachment strength of the communities. Also, some degradation of the underlying layers may have contributed to this loss. At such high levels of biomass, extreme attenuation of light through the mat can occur (e.g., 95% of incoming irradiance, Dodds 1989) which could result in light limitation and eventually senescence of the underlying layers. At the time when the low and high velocity communities were sloughing in the Okuku River, the medium biomass communities continued to grow and had not reached a peak in biomass by Day 92 (Fig. 4.2). However, the rate of average biomass accumulation had decreased substantially after Day 77 suggesting that at this point the rate of organic matter detachment by shear stress was starting to approach the rate of production.

Some differences were found between the New Zealand and Norwegian rivers. One clear difference was that colonization was slower in the New Zealand river. A possible explanation for this is that the more unstable bed in the Okuku River resulted in a more severe disturbance during the re-set flooding event. Stevenson (1990) has suggested that the duration of colonisation depends to some extent on the magnitude of the foregoing disturbance. The next clear difference

between the two rivers appeared during the period of exponential growth, when increasing velocities in the Okuku River resulted in a higher net growth rate, but in the Sokna a lower net growth rate occurred with increasing velocities. There are several likely explanations for this. First, the River Sokna was much deeper and steeper, and the average shear stress to which the periphyton community was exposed was therefore about 10 times higher (Table 4.1). Second, the difference in growth rate response could reflect the different growth forms of the communities in each river. The community in the Okuku was generally dominated by prostrate diatoms and it was not until near peak biomass was attained that filamentous algae appeared. In contrast, communities in the Sokna, and in many other studies where a negative correlation between biomass and velocity have been recorded (e.g., Lindstrom and Traaen 1984, Peterson and Stevenson 1990, Poff et. al. 1990), were dominated by sessile and filamentous taxa. These have greater form drag and skin friction because of the length of the filaments, and therefore they will be much more susceptible to higher shear stress (Chapter 3). These results suggest that shear stress may be a better parameter than mean velocity for discriminating the effects of spatial differences in hydraulics on stream periphyton.

Horner and Welch (1981) suggested that the influence of velocity on periphyton accrual changes depending on ambient nutrient concentrations. I agree with this and suggest that the differences in growth rates with higher velocities in the study rivers may also reflect differences in nutrient availability. I speculate that if nitrogen and/or phosphorus are present at high enough concentrations this will facilitate high exchange through the nutrient depleted laminar boundary layer, and within the mat, regardless of velocity effects. In other words, if saturation of growth rates occurs by high nutrient concentrations alone, higher velocities cannot enhance mass transfer further. In such circumstances, increases in velocity will only act negatively on the periphyton community by increasing shear stress and the rate of organic matter export. This will result in an overall negative relationship between peak biomass and velocity (e.g., Biggs and Gerbeaux 1993). Indeed, in a laboratory flume study, Horner et al. (1990) found that the positive effect of increased velocities on periphyton was more evident at low ($< 7.5$ mg $l^{-1}$) dissolved inorganic P concentrations than at higher concentrations. They therefore concluded that higher velocities benefitted periphyton in nutrient-poor streams.

The finding of an interaction between stage of community accrual and hydraulic conditions confirms that periphyton communities can have a high degree of spatio-temporal variability. It also supports the often-held notion that physical heterogeneity of stream environments contributes directly to patchiness of streambed communities (e.g., Pringle et al. 1988) and has important implications for assessing availability and predictability of food resources for invertebrate grazers. Many invertebrate taxa have fixed habits or limited mobility (e.g., some caddis larvae), and are unable to track these velocity mediated spatial changes in periphyton food resources around the streambed. It is conceivable that this leads to bursts of satiated growth, interspersed with prolonged periods of food limitation in different patches depending on local hydraulic conditions. The heterogeneous distribution of currents may also determine where different grazers can travel because of drag effects. Thus, Poff and Ward (1992) demonstrated that velocities and periphyton resources both mediated the foraging activity of a mobile grazing caddisfly.

The development of hydraulic habitat suitability curves specific to different stages of accrual for stream periphyton is an important step toward assisting the management of flow regimes for the maintenance of biodiversity in streams. However, it should be recognised that these have been established under conditions of moderate nutrient concentrations and low invertebrate grazing activity. Thus, they only define "potential" habitat suitability for different stages of community accrual. Eventually, it may be possible to incorporate the effects of other regulators of growth and biomass such as variable nutrients, grazing and flood frequency in dynamic models. Only then will it be possible to make specific predictions about periphytic biomass as a function of changes in hydraulic conditions in streams.

## VII. Summary

The aim of this aspect of my studies was to determine how long it can take for periphyton redevelopment following flood disturbance and how this varies according to spatial differences in water velocity around the streambed. Sites in two rivers were sampled for periphyton biomass

and associated water velocities at weekly or bi-weekly intervals for 90 - 110 days following flood events. No differences in biomass could be detected among low, medium and high velocity habitats in the early stages of recolonisation. However, at the end of the colonisation period differences were found with biomass being highest at low velocities (< 0.3m $s^{-1}$) and lowest at high velocities (>0.7 m $s^{-1}$). In one river (Okuku) a reversal of this trend occurred during the exponential growth phase with higher growth rates being recorded at higher velocities. Thus, at the time of peak biomass (Day 77), the highest biomass was recorded at high velocities and lowest biomass at low velocities ($P < 0.05$). Subsequently, sloughing occurred at high velocities, but the intermediate velocity communities continued to accrue and at the end of the sampling period they had the highest biomass. When the communities reached maturity (Day 92) biomass was unimodally distributed with a peak in AFDM at 0.5 - 0.7 m $s^{-1}$. Contrary to these results, the periphyton biomass in the second river (Sokna) continued to be higher in low velocity areas during the exponential growth phase. A new spate occurred before the peak biomass was reached in that river.

## VIII. References

APHA 1985. *Standard Methods for the Examination of Water and Wastewater.* American Public Health Association, Washington, DC.

Biggs, B. J. F. 1996. 'Hydraulic habitat of plants in streams', *Regul. Riv.,* **12,** 131-144.

Biggs, B. J. F. and Gerbeaux, P. 1993. 'Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand', *N.Z. J. Mar. Freshw. Res.,* **27,** 39-53.

Biggs, B. J. F. and Price, G. M. 1987. 'A survey of filamentous algal proliferations in New Zealand rivers', *N.Z. J. Mar. Freshw. Res.,* **21,** 175-191.

Dodds, W. K. 1989. 'Photosynthesis of two morphologies of *Nostoc parmelioides* (Cyanobacteria) as related to current velocities and diffusion patterns', *J. Phycol.,* **25,** 258-262.

Horner, R. R. and Welch, E. B. 1981. 'Stream periphyton development in relation to current velocity and nutrients', *Can. J. Fish. Aquat. Sci.,* **38,** 449-457.

Horner, R. R., Welch, E. B., Seeley, M. R., and Jacoby, J. M. 1990. 'Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration', *Freshwater Biol.,* **24,** 215-232.

Kamphake, L. J., Hannah, S. A., and Cohen, J. M. 1967. 'Automated analysis for nitrate by hydrazine reduction', *Water Research,* **1,** 205-216.

Lindstrom, E. A. and Traaen, T. S. 1984. 'Influence of current velocity on periphyton distribution and succession in a Norwegian soft water river', *Verh. Internat. Verein. Limnol.,* **22,** 1965-1972.

Lock, M. A. and John, P. 1979. 'The effect of flow patterns on uptake of phosphorus on river periphyton', *Limnol. Oceanogr.*, **24,** 376-383.

McIntire, C. D. 1966. 'Some effects of current velocity on periphyton communities in laboratory streams', *Hydrobiol.*, **27,** 554-570.

Norusis, M. J. 1992. *SPSS for Windows. Base system user guide. Release 5.0.* SPSS Inc.

Peterson, C. G. and Stevenson, R. J. 1990. 'Post-spate development of epilithic algal communities in different current environments', *Can. J. Bot.*, **68,** 2092-2102.

Poff, N. L., Voelz, N. J., and Ward, J. V. 1990. 'Algal colonization under four experimentally-controlled current regimes in a high mountain stream', *J. North Am. Benthol. Soc.*, **9,** 303-318.

Poff, N. L. and Ward, J. V. 1992. 'Heterogeneous currents and algal resources mediate in situ foraging activity of a mobile stream grazer', *Oikos,* **65,** 465-478.

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., Welcomme, R. L., and Winterbourn, M. J. 1988. 'Patch dynamics in lotic systems: the stream as a mosaic', *J. North Am. Benthol. Soc.*, **7,** 503-524.

Rorslett, B., Green, N., and Kvalvagnaes, K. 1978. 'Stereophotography as a tool in aquatic biology', *Aquat. Bot.*, **4,** 73-81.

Rorslett, B., Johansen, S. W., and Blakar, I. A. 1989. *Biologiske effekter i Suldalsvassdraget fra Ulla-Forre utbyggingen.* NIVA-rap nr.0-88050 (in Norwegian), Oslo.

Stevenson, R. J. 1983. 'Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration', *Ecology,* **64,** 1514-1524.

Stevenson, R. J. 1990. 'Benthic algal community dynamics in a stream during and after a spate', *J. North Am. Benthol. Soc.*, **9**, 277-288.

Stevenson, R. J. 1996. 'The stimulation and drag of current' pp. 321-340 in Stevenson, R. J., Bothwell, M. L., and Lowe, R. L. (Eds.), *Algal Ecology: Freshwater benthic Ecosystems.* Academic Press, San Diego. 753pp

Stevenson, R. J. and Glover, R. 1993. 'Effects of algal density and current on ion transport through periphyton communities', *Limnol. Oceanogr.*, **38**, 1276-1281.

Stevenson, R. J. and Peterson, C. G. 1989. 'Variation in benthic diatom (*Bacillariophyceae*) immigration with habitat characteristics and cell morphology', *J. Phycol.*, **25**, 120-129.

Stokseth, S. 1994. 'Hydrofysiske Forhold Og Begroing I Naturlige Elver'. Doktor Ingenior Avhandling Thesis, Institutt for Vassbygging, Unit-NTH, Trondheim. 131 p.

Whitford, L. A. and Schumacher, G. J. 1961. 'Effect of current on mineral uptake and respiration by a fresh-water alga', *Limnol. Oceanogr.*, **6**, 423-425.

Wilkinson, L. 1990. *SYSTAT: The system for statistics.* SYSTAT Inc, Evanston IL.

# Chapter 5

## Climax community development as a function of spatial variance in hydraulics of a regulated river

**Preface**

This study extends the work described in Chapter 4 by analysing in more detail post-disturbance peak biomass responses of periphyton to spatial variations in hydraulic conditions in a third river. Periphyton species composition, chlorophyll *a* concentration, organic matter biomass, and metabolic activity were analysed at a site in the Ohau River, a regulated river with low nutrient concentrations to investigate both population and community level responses to spatial gradients in hydraulic conditions. Three sets of stones, varying in periphyton biomass, were also incubated in a benthic respirometer equipped with a variable speed pump and in-line flow meter to determine the effects of varying velocity on community photosynthesis and respiration. This manuscript has now been published in *Freshwater Biology* **32**:49-59.

## I. Introduction

Increasing emphasis has been placed on the role of hydraulic features in determining the spatial distribution of organisms in streams (e.g. Statzner, Gore & Resh, 1988; Davis & Barmuta, 1989; Young, 1992). Flowing water can potentially affect periphyton through two conflicting processes (see Chapter 4). First it can increase metabolic rates (and possibly production) by controlling the thickness of the diffusive (laminar) boundary layer which can resist transfer of metabolites to and from cells (Whitford & Schumacher, 1961; Lock & John, 1979; Riber & Wetzel, 1987). Second, as water velocity increases, so does skin friction and drag on the periphyton community, and the shape, size, and orientation of organisms in the flow becomes very important in their bid to hold station (Vogel, 1981). If the drag induced by development of a mat exceeds its own tensile strength, it will be torn from the stream bed.

A large number of empirical studies have been carried out in experimental systems on the interaction between low flow water velocity and periphyton (e.g. Horner, Welch & Vennestra, 1983; Reiter & Carlson, 1986; Steinman & McIntire, 1986; DeNicola & McIntire, 1990; Peterson & Stevenson, 1990; Poff, Volez & Ward, 1990). A number of field manipulations and correlative studies have also been performed with artificial (e.g. Lamb & Lowe 1981, 1987; Korte & Blinn, 1983; Stevenson 1984) and natural (Chapter 4) substrates. However, obtaining clear evidence of a shift from diffusion to shear stress limitation as a function of velocity from these studies has not been easy because of the complex interaction of hydraulics with successional stage (i.e. age) of the community (Chapter 4), physiognomy, the state of the nutrient pool, and the effect of feedback whereby the developing community alters its own micro-hydraulic environment (Reiter, 1989).

To help biological interpretation of the hydraulic classification of habitats, as discussed by Davis & Barmuta (1989) and Young (1992), and to develop tools such as hydraulic habitat preference curves (e.g., Jowett et al., 1991) for prediction of the effects of flow regulation/abstraction on periphyton, a greater understanding is needed of relationships between naturally occuring periphyton and the hydraulic features of streams. Knowledge of these relationships should also give a better understanding of the importance of the spatial component of stream hydraulics (cf. the temporal component; Chapters 2, 3, and 4) on periphyton development. The objective of the present study was to analyse community characteristics along a hydraulic gradient using natural field communities on natural substrates to see how

parameters such as species composition, chlorophyll *a* concentration, organic matter biomass, and primary productivity change in response to hydraulic stress. Data were then categorised according to the hydraulic parameters of the habitats, so that the characteristics of pools, runs and riffles could be compared. No previous periphyton studies have analysed responses of naturally occurring communities along a continuous hydraulic gradient, nor related the data to the spatial occurrence of micro-habitat hydraulic features in streams. The hypothesis tested was that a normal distribution in abundances of taxa and biomass should occur along the gradient, but that the central tendencies should be significantly different among taxa reflecting their different metabolic/tensile strength optima. Low growing prostrate taxa were expected to dominate high velocity areas of the river (Lamb & Lowe 1981; Stevenson & Peterson, 1989; Peterson & Stevenson, 1990), grading to large celled, upright, taxa in low velocity areas (e.g. Poff et al., 1990). The confounding effects of differing nutrient concentrations, stages of accrual, and experimental artifacts were factored out by confining the study to a small reach of a stream with a constant nutrient and flow regime that was regulated following a major re-setting flood event, and by sampling natural substrata.

## II. Study area

The study was carried out at a single site in the Ohau River, South Island, New Zealand. The Ohau flows from Lake Ohau, a large oligotrophic lake, which at the time of sampling (February 1990) was regulated at a constant flow of 1 $m^3$ $s^{-1}$. Sampling was carried out 6 weeks after a 9.1 $m^3$ $s^{-1}$ flood event which was expected to have sloughed most periphytic growth from the bed (Biggs & Close 1989). The communities appeared to be approaching peak biomass on the accrual cycle at the time of sampling since there was high biomass present, but no obvious spontaneous sloughing. The water was low in nutrients. Median values for water quality variables based on bi-weekly sampling over a 12 month period encompassing the time when the present study was carried out were: 4.96 mS $m^{-1}$ conductivity, 2.5 mg $m^{-3}$ DRP, 7 mg $m^{-3}$ $NH_4$-N, 24.4 mg $m^{-3}$ $NO_3$-N, and a DRP:TIN ratio of 13.0 (authors' unpublished data). Median water temperature was 13.1 $^oC$.

## III. Methods

*Field procedures*

The study reach was approximately 80m long and 10m wide. Sampling was based on a matrix of depths and velocities. This strategy was adopted because random sampling gives data which reflect the natural distribution of depths and velocities, thus any organism preferences will not be independent of the frequency with which the most common habitats are sampled. Samples from 12 velocity increments (defined in 0.1 m $s^{-1}$ intervals) were obtained in the 0.1 - 1.5 m $s^{-1}$ range, at each of 5 (0.1m) depth increments between 0.1 - 0.5m. For example, if the measured velocity was 0.83 m $s^{-1}$ then the sample taken at that point was allocated to the 0.8 - 0.9 m $s^{-1}$ increment and grouped with other data from that range (see below for a description of replication).

Depth and velocity were measured using an electro-magnetic current meter and wading rod. All velocity measurements were taken at 0.6 of depth. Comparable depths and velocities were present for at least 2m upstream of a sampling point.

Three spatially separate stones were obtained for each depth and velocity combination to give three independent replicates. These three replicates were then pooled to give a single data point for each hydraulic combination. All sampling was carried out on the same day. A 48 mm diameter circle was scribed on the top of each cobble and all material was scraped from within this area using a scalpel. All cobbles had smooth surfaces. Periphyton samples were placed in individual polyethylene containers with river water and chilled for approximately 5 hours before freezing.

Froude number (Fr) for the sampling points was calculated as:

$$Fr = V/(Dg)^{0.5} \qquad (1)$$

where V = mean water column velocity (m $s^{-1}$), D = depth (m), and g = acceleration due to gravity (9.81 m $s^{-2}$) (Dingman, 1984). Froude number normalises velocity according to depth and is probably a better surrogate of shear velocity than mid-column velocity. Habitats where $Fr < 0.18$ were classified as pools, $Fr = 0.18 - 0.41$ runs, and $Fr > 0.41$ riffles after Jowett (1993).

Photosynthesis and respiration of periphyton were measured in a sealed plexiglass chamber (Hickey, 1988) with recirculating water (internal dimensions of chamber = 0.16 x 0.38 m) which was submerged in a 0.3m deep run at the site to maintain ambient temperature. Water was pumped around the system with a large

(0.75 x 1.5 m frame dimensions) variable speed centrifugal pump capable of delivering 75 l $s^{-1}$. Flow rates through the chamber were monitored continuously with a Quasar model P58440 in-line flow meter (Signet Scientific, El Monte, California). Based on the cross-sectional area of the chamber, and flow rate, boundary velocities of 0.14 - 0.38 m $s^{-1}$ were simulated.

Three separate metabolic experiments were carried out. For each experiment a set of five to eight flat topped cobbles was chosen from a depth of 0.3 m and a velocity of 0.2 - 0.3 m $s^{-1}$. Community development was visually similar within the set, but the sets covered the range of biomasses observed in the matrix sampling for the given depth/velocity regime (see Fig. 5.3). Cobbles were enclosed in the chamber so that their upper surfaces lay parallel to the streamflow and just protruded into the upper half of the chamber.

Dissolved oxygen (DO) within the chamber was monitored using a YSI - DO probe inserted in the flow line. A scaling amplifier was used to subtract background oxygen concentration and amplify the working range (usually 1 mg $l^{-1}$) to full scale. After net production (NP) was measured the water in the system was completely renewed and an opaque cover placed over the chamber so that community respiration (CR) could be measured in the same way. Gross production (GP) was assessed as the sum of CR and NP. While three production experiments were commenced, one was abandoned because the river DO concentration was too high at the time and spontaneous degassing was occurring after only the second velocity increment.

At the completion of each experiment the entire surface area of each cobble in the chamber was scrubbed free of periphyton in 2 l of river water as described by Biggs & Close (1989). This sample was then returned to the laboratory for determination of AFDM and chlorophyll *a* (see below). Volumes and surface areas of the cobbles were determined (Dall 1979) to correct the chamber volume. Stream-bed area occupied by these stones was calculated to be 31.5% of the sum of the individual stone surface areas on the assumption that: a) the area of cobbles exposed to the overlying flow was half their total surface area on average, and b) the bed area occupied by the stones was 63% of the exposed stream bed area (Quinn, 1985). Photosynthesis and respiration of plankton/seston were not measured separately, but were probably negligible compared with benthic metabolism in this oligotrophic water. Ambient stream temperature during these experiments was 15 - 22 $^{o}$C.

*Laboratory procedures*

Each periphyton sample was thawed and homogenised using a blender (Biggs, 1987). The sample was then transfered to a narrow necked bottle, brought to a known volume, and shaken thoroughly to obtain a suspension from which a subsample was withdrawn. The abundance of taxa was assessed by scanning sub-samples under 100 to 790 magnification using an inverted microscope and scoring the relative biovolume of each taxon on an eight-point scale (1, low to 8, dominant). In most samples two or, at the most, three taxa made up over 80% of the biovolume. Further details, and the taxonomic references used, are given by Biggs (1990).

Three 5 ml aliquots per sample were removed from the sample suspension and pooled for spectrophotometric analysis of chlorophyll *a* using boiling 90% ethanol as extractant, correcting for phaeopigments by acidification, and employing a chlorophyll *a* co-efficient of 28.66 (Sartory & Grobbelaar, 1985). A further three aliquots were removed in the same way for determination of ash-free dry mass (AFDM) by drying at 105 $^{o}$C for 24 h and ashing at 500 $^{o}$C for 4 h.

A measure of the percentage of the mat composed of chlorophyll *a* was calculated as chlorophyll *a* divided by AFDM (both in milligrams) times 100.

*Data analysis*

Results were analysed by scatter plots with trends being defined by a locally weighted average smoothing line (SMOOTH=LOWESS, in SYSTAT (Wilkinson, 1990)). Pearson correlations were used to define 'goodness-of-fit' for near linear relationships, and least-squares regression to estimate parameters for linear models.

## IV. Results

*Species responses*

The diatom *Cymbella kappii* Cholnoky dominated the communities (relative biovolume rating = 8) most frequently, with *Synedra ulna* (Nitzsch) Ehr and *Gomphoneis herculeana* (Ehr) Cleve being co-dominant or abundant (relative biovolume rating = 7). Abundances of minor taxa are not considered further. The relative biovolumes of two of these three common taxa did not change in response to the 0.1 - 1.5 m $s^{-1}$ velocity gradient or the 0.01 - 1.5 Fr gradient (Fig. 5.1). There was no structural change toward a community dominated by low growing prostrate taxa at high velocities. Only *Gomphoneis herculeana* showed any velocity preference (albeit weak) with highest relative biovolumes in the 0.8 - 1.2 m $s^{-1}$ range.

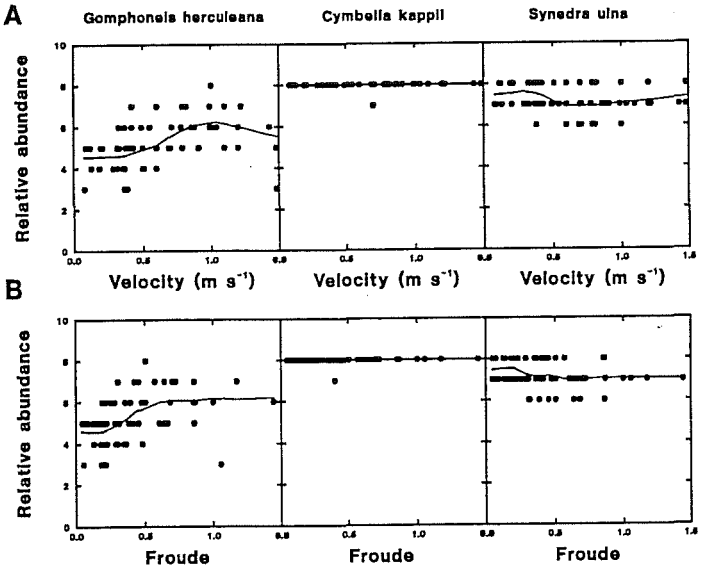


Fig. 5.1. Relative biovolume of the three most common taxa as a function of velocity (A) and Froude number (B). The solid line is the locally weighted average smoothing line (see Methods).

However, physiognomic changes were apparent in response to velocity and Fr gradients. Large quantities of mucilage, which appeared to originate from *Cymbella kappii* and *Gomphoneis herculeana*, were present in the samples taken from higher velocities. It was not possible to quantify this, or the relative differences in stalk lengths between velocities, since this material was composed of a matrix of entangled non-structural mucilages. However, some individual *Gomphoneis herculeana* stalks which could be separated were over 2 mm long (i.e. 20 times the maximum length of the cells) (Fig. 5.2). Stalks in low velocity areas were less than 0.5mm long.


Fig. 5.2: Scanning electron micrographs of *Gomphoneis herculeana* illustrating the size and number (including branching) of stalks developed under high velocities in the Ohau River. (a) A single *Gomphoneis herculeana* cell in girdle view with elongated stalk; (b) branched *Gomphoneis* stalks with cell heads.

*Biomass responses*

AFDM was relatively invariate in the 0.1 - 0.4 m $s^{-1}$ range (Fig. 5.3). However, from 0.5 to 1.5 m $s^{-1}$ it increased greatly. Overall, there was a highly significant positive correlation between AFDM and water velocity (Fig. 5.3; $r$=0.735, $P$<0.001). The best-fit regression model for this was:

$$\text{Ln AFDM} = 1.048 + 0.897 * \text{velocity} \qquad r^2=0.578 \qquad (2)$$

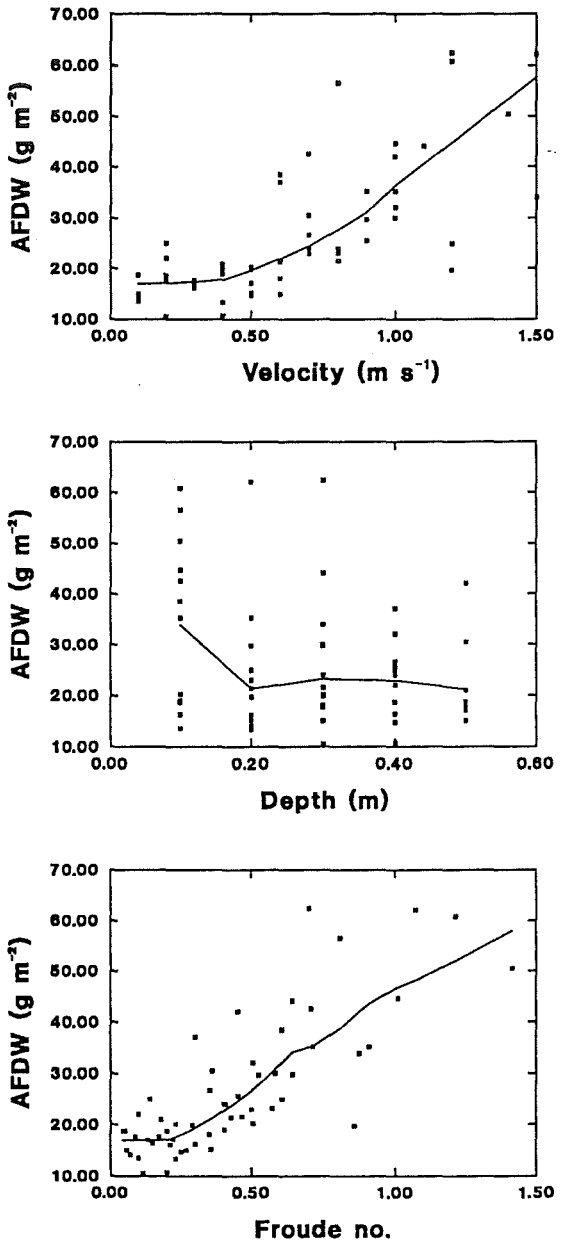


Fig. 5.3: AFDM of periphyton on cobbles in the Ohau River as a function of hydraulic habitat parameters. The solid line is the locally weight average smoothing line (see Methods).

While the correlation between AFDM and depth was significant ($r$= -0.282, $P$=0.035) the main change occurred in the 0.1 to 0.2 m depth range and not across the whole depth gradient (Fig. 5.3). However, there was a strong correlation between AFDM and Fr ($r$=0.797, $P$<0.001). The regression equation for this relationship was:

$$AFDM = 2.475 + 7.235 * Fr \qquad r^2=0.635 \qquad (3)$$

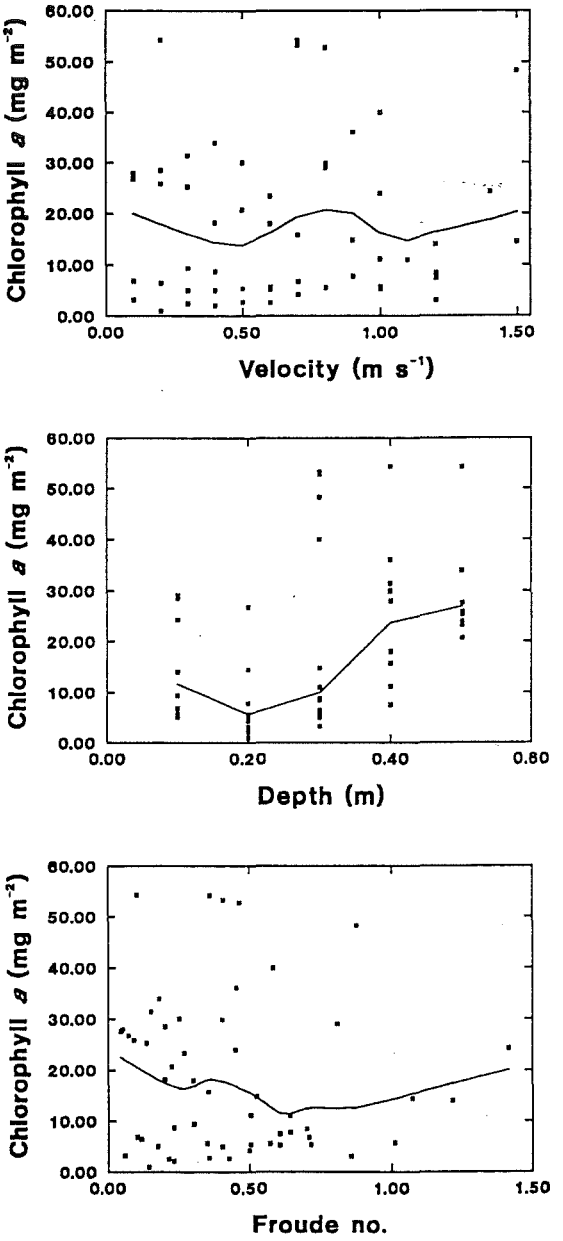


Fig. 5.4. Chlorophyll *a* concentration on cobbles in the Ohau River as a function of hydraulic habitat parameters. The solid line is the locally weight average smoothing line (see Methods).

Chlorophyll *a* did not display any trend with velocity or Fr (Fig. 5.4). Since the same three taxa generally dominated all communities, this finding suggests that a similar number of viable algal cells was present over the entire hydraulic gradient. However, chlorophyll *a* was significantly correlated with depth ($r$=0.487, $P$<0.001).

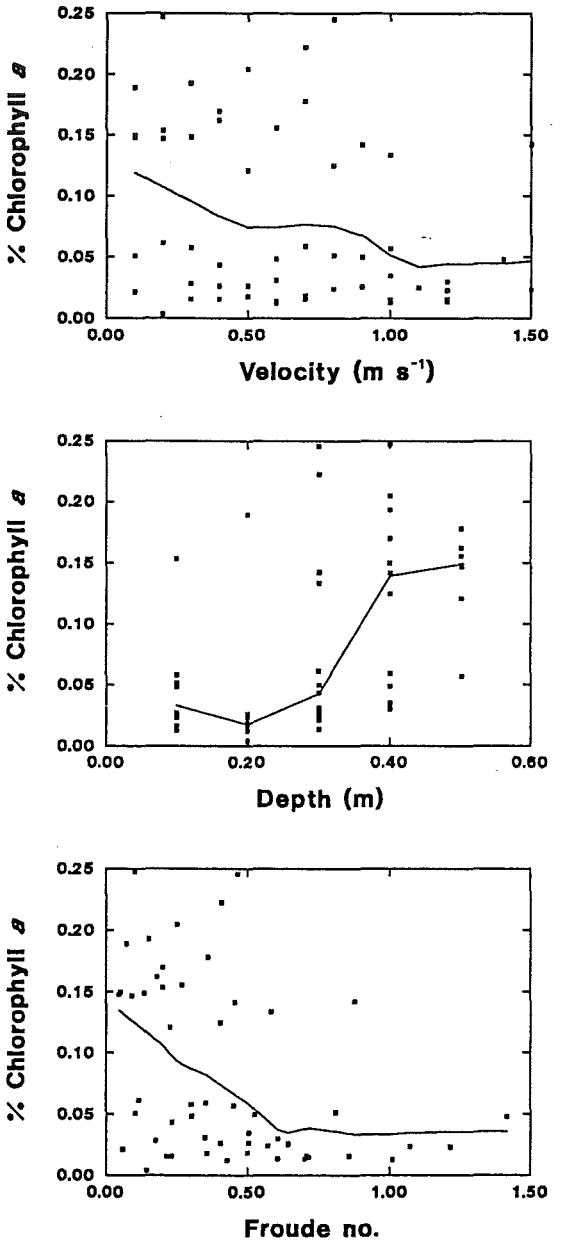


Fig. 5.5. Chlorophyll *a* as a percentage of periphyton biomass (AFDM) on cobbles in the Ohau River as a function of hydraulic habitat parameters. The solid line is the locally weight average smoothing line (see Methods).

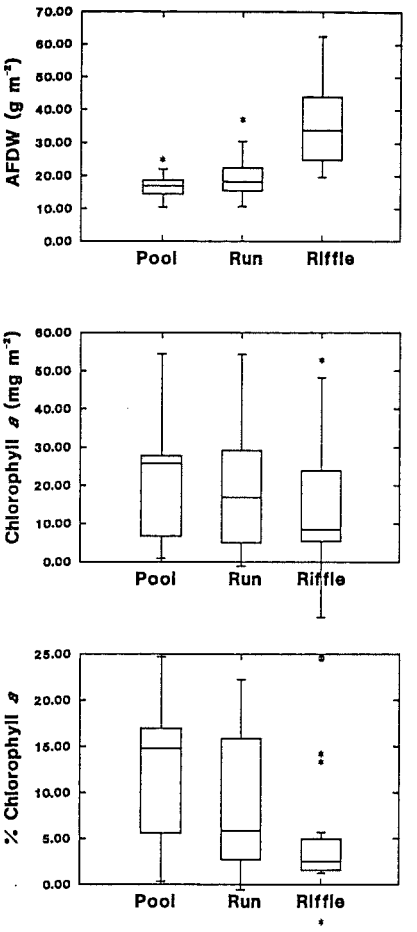


Fig. 5.6. AFDM, chlorophyll *a* and chlorophyll *a* as a percentage of biomass grouped into pool, run, and riffle habitats on the basis of Froude numbers. The bars within the boxes define median values, the limits of the boxes define one quartile and the error bars are 1.5 times the interquartile range (see Wilkinson 1990, SYGRAPH manual p.166).

A negative correlation was found between water velocity and the percentage of biomass composed of chlorophyll *a* ($r$= -0.278, $P$=0.038; Fig. 5), and can be attributed to the relatively invariate chlorophyll *a* concentration, but increasing AFDM at higher velocities. Percentage chlorophyll *a* generally increased with depth ($r$=0.558, $P$=0.001) although most of the difference was attributable to the 0.4 and 0.5 m deep communities. As with chlorophyll *a* concentration, there was a large scatter in percentage chlorophyll *a* at low Fr, and less scatter at high Fr. Overall, there was a significant negative correlation between percentage chlorophyll *a* and Fr ($r$= -0.412, $P$=0.002).

The samples were grouped in terms of spatial variability in hydraulic conditions into pool, run, and riffle categories according to the Fr number classification of Jowett (1993). Significant differences occurred for AFDM and percentage chlorophyll *a* across these categories (Kruskal-Wallis ANOVA, $P$<0.05) with AFDM highest in the riffles and lowest in the pools (Fig. 5.6). The converse applied for percentage chlorophyll *a*. AFDM was least variable in the pool habitat class, whereas percentage chlorophyll *a* was most variable there. Once again, the converse applied for the riffle habitat.

*Metabolic responses*

The three mats used in the metabolic experiments were 1.0, 1.9, and 4.8 mm thick and had AFDM values of 9.7, 11.3 and 24.1 g $m^{-2}$, respectively. These covered the full range of development recorded in the matrix sampling over the velocity range 0.20 - 0.30 m $s^{-1}$ (Fig. 5.3). For the 11.3 g $m^{-2}$ mat, production exceeded respiration at the calculated stream boundary velocity (GP/CR approximately 1.3, Fig. 5.7). However, for the high biomass mat, respiration greatly exceeded production (GP/CR approximately 0.5).

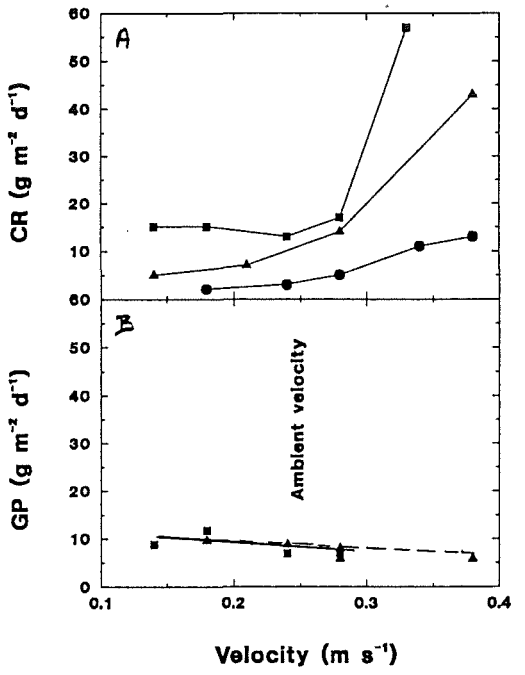


Fig. 5.7. Response of periphyton respiration (A) and gross production (B) to velocity in the benthic respirometer (dots = 9.7 g $m^{-2}$ AFDM community, triangles = 11.3 g $m^{-2}$ AFDM community, squares = 24.1 g $m^{-2}$ AFDM community; dashed line on figure B is the best fit for the triangle points).

GP was very similar for two of the mats (the experiment for the third was unsuccessful due to spontaneous degassing in the chamber) and relatively invariate with increasing velocity (possibly dropping slightly) (Fig. 5.7). In contrast, CR increased greatly with an increase in AFDM biomass of the mat. For each mat CR also increased with velocity and the magnitude of this change increased as biomass increased.

## V. Discussion

Sampling periphyton communities of known, uniform, age on natural substrata in a regulated stream should provide ideal conditions to establish hydraulic habitat preferences for periphyton species. Such an approach avoids many of the confounding influences of periodic disturbances and flow pulsing found in unregulated streams, and sloughing/regrowth associated with older communities.

Unexpectedly, I found the same diatoms dominating or abundant over the entire hydraulic gradient, and only for *Gomphoneis herculeana* was there any suggestion that cells were more abundant within a specific velocity range. Thus, the hydraulic heterogeneity of the stream bed was not leading to a 'patch-work' of community types as was expected given that periphyton species can show distinct velocity preferences (e.g., Poff et al. 1990); nor was there a demonstration of selection based on size/adhesion habits such as low profile adnate taxa being more prominant at higher velocities (e.g., Lamb & Lowe, 1981; Korte & Blinn, 1983; Peterson & Stevenson, 1990). The dominant taxa at the study site monopolized stone surfaces over a wide range of velocity conditions resulting in many aspects of the original hypotheses not being supported.

There were, however, progressively higher accumulations of organic matter (mainly mucilage; as shown by microscope analysis, and AFDM - percentage chlorophyll *a* results) when velocities exceeded 0.4 m $s^{-1}$. This was unexpected from theory (outlined in the Introduction), experimental studies which have demonstrated that high velocities result in thinner algal mats than low velocities (e.g. Reiter & Carlson 1986), and the results of work reported in the previous chapter (Chapter 4).

In contrast, chlorophyll *a* and gross primary production did not vary greatly with water velocity, nor with AFDM of the mat. However, respiration did increase with velocity, and the GP/CR ratio decreased, with higher mat development showing that some metabolic response to higher velocities could occur. This was probably through increased oxygen penetration of the mats at higher turbulence. These data provide further evidence that the high AFDM communities were composed predominantly of non-phototrophic materials, and also suggest that the actively growing cells were probably located at the surface of the mat.

The quantity of mucilage accumulated by the communities was remarkably high. It does not seem plausible that these mucilaginous accretions, which exceeded 10 mm in thickness at high velocities, were just produced by stalk elongations in *Gomphoneis herculeana* (maximum observed stalk lengths were around 2 mm). There must have been considerable extracellular secreted material as well. The secretion of mucilage by diatoms for non-structural features is generally low during exponential growth, but increases significantly during stationary, nutrient-limited growth (such as high phophorus:nitrogen ratios, see review by Hoagland et al. 1993). How this was being affected by increases in water velocity in this study is unknown since photosynthetic rates, which I assume would drive such polysaccharide synthesis, did not respond to velocity manipulations up to 0.38 m $s^{-1}$ (Fig. 5.7). It is possible that if higher velocities could have been achieved in my experiments, a photosynthetic response may have been recorded. AFDM did not show a response until velocities exceeded 0.4 m $s^{-1}$ although the main photosynthetic response to velocity change had been expected in the 0 - 0.3 m $s^{-1}$ range (Whitford & Schumacher, 1961; Lock & John, 1979).

The effect of environmental stress on mucilage accumulation is not well understood (Hoagland et al. 1993). However, Roemer, Hoagland & Rosowski (1984) have reported high mucilage accumulation on artificial substrata anchored just 0.8 m below the surface in a reservoir where *Cymbella affinis* (probably the same as *Cymbella kappii*) and *Gomphonema olivaceum* were dominant. Furthermore, Peterson (1987) found that mucilage production was induced in response to stress resulting from periodic desiccation. Such accumulation would probably assist hydration characteristics of the mat. For the communities in my study, the eco-physiological advantages that these secretions confer are unclear. However, it is possible that algal species were also modifying their local micro-hydraulic environments with these mucilages as has been shown experimentally (Reiter 1989). If mucilages were smoothing out surface irregularities on the substrata (especially when it was over 10 mm thick) it could improve the growth environment by reducing turbulence and form-drag.

The finding of much higher periphytic AFDM in habitats classified as riffles than runs or pools (Fig. 5.6) concurs with differences in accumulation of organic matter that have been observed elsewhere in New Zealand's nutrient poor cobble and gravel-bed rivers (author's unpublished observations; Scarsbrook & Townsend, 1993). If mucilagenous material can be used as food by invertebrates it would enhance the

richness of riffle habitats for higher trophic levels. Indeed, some insects, particularly chironomids, were observed in this matrix at very high densities.

The in-stream flow incremental methodology for predicting the effects of flow change on aquatic environments has encouraged the study of in-stream habitat suitability functions for many aquatic organisms (e.g. Jowett et al., 1991). This is with the expectation that changes in in-stream habitat with flow (as predicted by hydraulic modelling) will result in changes in species abundances. In the present study it was not possible to demonstrate clear hydraulic preferences for periphyton taxa, nor for live periphytic biomass. Equations (2) and (3) depict relationships that could be useful for approximating AFDM levels within similar nutrient poor streams following extended periods of stable flow. Further, the grouping of both AFDM and chlorophyll *a* by habitat type gives an indication of differences in magnitude of these parameters for different hydraulic habitat features. Nevertheless, a great deal more work is required on naturally occurring periphyton before precise relationships between periphyton and hydraulic parameters can be developed, and my results suggest that AFDM and chlorophyll *a* should be treated as quite distinct community attributes.

Heterogeneous channel configurations result in a wide gradient of hydraulic stress over small spatial scales. Habitats such as pools and riffles represent extremes along this continuum. This study has shown that the responses of periphytic algae to hydraulic habitat features in streams are complex and that it may be difficult to develop hydraulic habitat preference curves for periphyton communities. Some taxa have the strong physiological plasticity needed to cope with hydraulic extremes.

## VI. Summary

The aim of this aspect of my studies was to analyse in more detail post-disturbance peak biomass responses of periphyton to spatial variations in hydraulic conditions. Sampling was carried out in a regulated river 6 weeks after a flood. The communities were dominated by diatoms over the full range of hydraulic conditions incorporated in the sampling (0 - 1.5 m $s^{-1}$ velocity). Unexpectedly, *Cymbella kappii* and *Synedra ulna* were dominant or co-dominant at all levels of velocity and Froude number (Fr). A third taxon which was very abundant, *Gomphoneis herculeana*, was most common within the mid-velocity range (velocity = 0.8 - 1.2 m $s^{-1}$). The physiognomy of the communities changed with a change in hydraulic conditions. Thus, progressively more diatom mucilage was found as velocity and Froude number

increased and consequently relatively thin films (1 - 2 mm) occurred at low velocities and Froude numbers (in pool habitats), and thicker (approximately 10 mm) mats were present at higher velocities and Froude numbers (in riffle habitats). Associated with this, ash-free dry mass (AFDM) increased strongly, but chlorophyll *a* concentration did not, resulting in a decrease in % of the mat composed of chlorophyll *a* over the gradient. Primary production-water velocity experiments conducted in an in-situ benthic chamber showed that gross production did not differ significantly between two communities of different biomass, and showed a slight downward trend over a velocity gradient (0.14 to 0.38 m $s^{-1}$). In contrast, community respiration increased greatly with mat biomass and also as a function of increased water velocity. The combined AFDM, chlorophyll *a*, and metabolism results suggested that the zone of photosynthesis was maintained at the surface of the mats with variable amounts of mucilage being secreted below depending on hydraulic conditions. Diatom communities demonstrated considerable physiognomic plasticity through the accumulation of mucilage. It is concluded that the response of periphyton to spatial differences in habitat hydraulics in streams is highly complex and it may be difficult to define clear hydraulic habitat preference curves for periphyton communities in nutrient poor streams.

## VII. References

Biggs, B.J.F. (1987) Effects of sample storage and mechanical blending on the quantitative analysis of river periphyton. *Freshwater Biology*, **18**, 197-203.

Biggs, B. J. F. (1990) Periphyton communities and their environments in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 367-386.

Biggs, B. J. F. & Close, M. E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs, B. J. F. & Gerbeaux, P. (1993) Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **27**, 39-53.

Dall, P. C. (1979) A sampling technique for littoral stone dwelling organisms. *Oikos*, **33**, 106-112.

Davis, J. A. & Barmuta, L J. (1989) An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshwater Biology*, 21, 271-282.

Dingman, F. (1984) *Fluvial hydrology*. W. H. Freeman Company, NY.

Hickey, C.W. (1988) Benthic chamber for use in rivers: testing against oxygen mass balances. *Journal of Environmental Engineering*, **114**, 828-845.

Hoagland, K. D., Rowsowski, J. R., Gretz, M. R., & Roemer, S. C. (1993) Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. Journal of Phycology, **29**, 537-566.

Horner, R. R., Welch, E. B., and Veenstra, R. B. (1983) Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. *Periphyton of freshwater ecosystems* (Ed R. G. Wetzel), 121-134. Developments in Hydrobiology, Junk.

Jowett, I. G. (1993) A method for objectively identifying pool, run, and riffle habitats from physical measurements. *New Zealand Journal of Marine and Freshwater Research*, **27**, 241-248.

Jowett, I. G., Richardson, J., Biggs, B. J. F., Hickey, C. W. & Quinn, J. M. (1991) Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitabiliy curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **25**, 187-199.

Korte, V. L. & Blinn, D. W. (1983) Diatom colonization of artificial substrata in pool and riffle zones studied by light and scanning electron microscopy. *Journal of Phycology*, **19**, **332-341**.

Lamb, M. A. & Lowe, R. L. (1981) A preliminary investigation of current speed on periphyton community structure. *Micron*, **12**, 211-212.

Lamb, M. A. & Lowe, R.L. (1987) Effects of current velocity on the physical structuring of diatom (Bacillariophyceae) communities. *Ohio Journal of Science*, **87**, 72-78.

Lock, M. A. & John, P. (1979) The effect of flow patterns on uptake of phosphorus on river periphyton. *Limnology and Oceanography*, **24**, 376-383.

Peterson, C. (1987) Influences of flow regime on development and desiccation response of lotic diatom communities. *Ecology*, **68**, 946-954.

Peterson, C. & Stevenson, R. J. (1990) Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Botany*, **68**, 2092-2102.

Poff, N. L, Volez, N. J. & Ward, J.V. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society*, **9**, 303- 318.

Quinn, J. M. (1985) *Wastewater effects on epilithon, particularly sewage fungus and water quality in the Manawatu River, New Zealand.* Unpublished PhD thesis, Massey University, Palmerston North, New Zealand.

Reiter, M. A. (1989) The effect of a developing algal assemblage on the hydrodynamics near substrates of different sizes. *Archive fur Hydrobiologie*, **115**, 221-244.

Reiter, M. A. & Carlson, M. A. (1986) Current velocity in streams and the composition of benthic algal mats. *Canadian Journal of Fisheries and Aquatic Science*, **43**, 1156-1162.

Riber, H. H. & Wetzel, R. G. (1987) Boundary layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnology and Oceanography*, **32**, 1181-1194.

Roemer, S. C., Hoagland, K. D. & Rosowski, R. J. (1984) Development of a freshwater periphyton community as influenced by diatom mucilages. *Canadian Journal of Botany*, **62**, 1799-1813.

Sartory, D. P. & Grobbelaar, J. U. (1984) Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, **114**, 117-187.

Scarsbrook, M. R. & Townsend, C. R. (1993) Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Statzner, B., Gore, J. A. & Resh, V. H. (1988) Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society*, **7**, 307-360.

Steinman, A. D. & McIntire, C. D. (1986) Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. *Journal of Phycology*, **22**, 352-361.

Stevenson, R. J. (1984) How currents on different sides of substrates in streams affect mechanisms of benthic algal accumulation. *Internationale Revue gesamten Hydrobiologie*, **69**, 241-262.

Stevenson, R. J. & Peterson, C. (1989) Variation in benthic diatom (Bacillariophyceae) immigration with habitat characteristics and cell morphology. *Journal of Phycology*, **25**, 120-129.

Vogel, S. (1981) *Life in Moving Fluids*. Princeton University Press.

Whitford, L. J. & Schumacher, G. J. (1961) Effects of current on mineral uptake and respiration by a freshwater alga. *Limnology and Oceanography*, **6**, 423-425.

Wilkinson, L. (1990) *SYSTAT: The system for statistics*. Evanston, IL: SYSTAT, Inc.

Young, W. J. (1992) Clarification of the criteria used to identify near-bed flow regimes. *Freshwater Biology*, **28**, 383-391.

# Chapter 6

## Disturbance - Resource Supply - Grazer Control of Stream Periphyton: A preliminary conceptual model

**Preface**

The results of the previous chapters have demonstrated the fundamental importance that hydraulic disturbance has in structuring periphyton communities in streams. In Chapter 2 it was also identified that limiting nutrient supply (i.e., resource availability) is important in determining inter-disturbance growth in un-shaded streams. Thus, the overall average biomass of periphyton in these un-shaded streams was jointly determined by disturbance frequency and nutrient supply. This result parallels certain components of terrestrial plant strategy theory (e.g., Grime 1979). In the following chapter I develop this concept further, addressing species performances in the context of disturbance and resource supply. Although not investigated for this thesis, I also attempt to integrate the effects of invertebrate grazing based on published information since grazing is also an important controller of periphyton biomass accrual in certain habitats. The overall objective is to develop a conceptual model of the main factors driving periphyton biomass accrual and species assemblages in stream ecosystems. Aspects of this model are then tested in Chapters 7 and 8.

## I. Introduction

Ecology is the scientific discipline that identifies and attempts to determine the causes of patterns in the distribution, abundance and dynamics of the Earth's biota (Tilman 1989). Patterns may occur in both space and time and are thought to reflect genetic traits to withstand, and exploit, spatio-temporal patterns in environmental conditions and resources. Southwood (1977, 1988) suggested that these patterns in habitat conditions could be viewed as a 'habitat template'. Determining the structural attributes of different parts of the template, and elucidating those species traits that enable different taxa to successfully exploit particular conditions, has long been a fundamental component of ecological research. Such knowledge is necessary in our bid to predict the structure and distribution of communities, and the impacts of environmental change.

*Structural attributes of the habitat template*

Research has proceeded in parallel in various environments (e.g. oldfields, streams etc) and on a range of groups of organisms (e.g. vascular plants, bryophytes, invertebrates etc.) to determine the fundamental attributes of habitats that control species membership and biomass development (e.g., Grime 1979, Grime et al. 1990, Hildrew and Townsend 1987, Townsend 1989, Townsend and Hildrew 1994). While explanations for some of the underlying mechanisms differ (e.g., competitive superiority as a function of resource capture: Tilman 1977, Grime 1979) considerable agreement exists as to the identity of many of the fundamental driving variables of ecosystems. These can be classified into two groups: firstly, those which promote the development of organisms (termed 'resources'). These include nutrients/food, space and light. Secondly, variables that cause the destruction of populations (termed 'disturbance'). Examples of factors causing disturbance include storms, fire, toxic chemical spills, and floods. Disturbance, while adversely affecting some species, may affect others positively by reducing competition and increasing resource supply (Pickett and White 1989). Grazing and predation are further mechanisms for population loss. However, at large scales these are usually not termed disturbance; grazing and predation are a long-term stress on populations, rather than a punctuated destruction. Many of the impacts of grazing may, however, be analogous to disturbance (e.g., Steinman et al. 1991, Peterson and Stevenson 1992).

Broad gradients in both resource supply and disturbance frequency/intensity occur in natural systems. Depicting these axes in two dimensional space enables the definition of a disturbance - resource supply habitat matrix (Fig. 6.1). It is likely that through

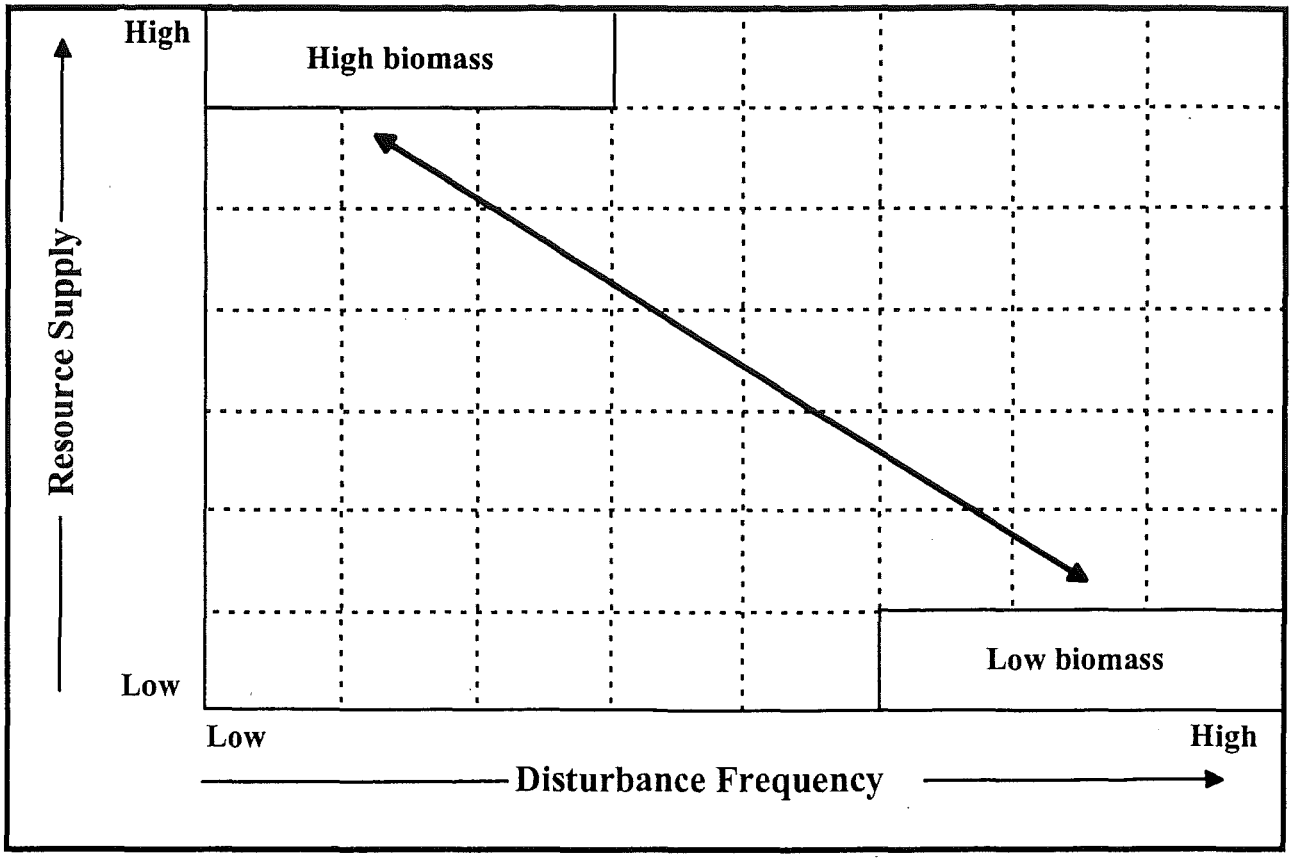


Fig. 6.1: A conceptual habitat matrix defined by gradients in disturbance frequency/intensity and resource supply. Each cell represents unique permutations of disturbance and resource supply. These effectively define niche dimensions.

natural selection different organisms will have evolved different sets of traits to enable survival and competitive success in specific cells of such a habitat matrix. Determining cell (or habitat) preferences for different species has been an important area of ecological research for many years. Grime (1979) identified four phenotypic traits of terrestrial vascular plants which were thought to control survival and competitive ability: morphology, life history, physiology, and miscellaneous attributes (such as resistance to consumption by unspecialised herbivores). These broad groupings are probably applicable to other plant groups (e.g. Grime et al. 1989) and possibly some animal groups too (e.g., Scarsbrook and Townsend 1993).

Changes in community species composition usually lead to changes in community biomass and functional processes. Based on the definition of disturbance ('the

mechanism which limits plant biomass by causing its partial or total destruction', Grime 1979), it is a truism that community biomass (the mean of the population responses) should always be low in highly disturbed environments (Fig. 6.1). Further, regular disturbance should select for a dominance by disturbance-resistant taxa or 'weedy'/resilient taxa with rapid colonisation and growth characteristics (e.g., flats in gravel bed rivers subject to annual flood disturbances, praries subject to summer wildfire). Conversely, high biomass will only be possible in habitats that lack regular disturbance. How much of this biomass potential is realized then becomes a major function of the degree of resource supply. Thus, habitats with low disturbance frequency and high resource supply have the most potential for a high carrying capacity (e.g., regions which develop rain forest) (Fig. 6.1). In habitats where disturbance frequency is low, and resource supply is also low, growth is usually slow and overall biomass accrual moderate to low (e.g., dry-land/desert regions) (see Grime 1979 for a full discussion of these concepts in relation to terrestrial plant distribution).

## II. Application of the disturbance - nutrient resource supply concept to stream periphyton

*Empirical evidence for disturbance - nutrient resource control of periphyton development in streams*

Extensive research over the last 20 years has clearly demonstrated that disturbance and nutrient resource supply are important determinants of stream periphyton development. Biomass can be severely reduced and taxonomic structure altered toward low-profile, tightly adhering taxa by flood disturbance (e.g., Douglas 1958, Tett et al. 1978, Fisher et al. 1982, Power & Stewart 1987, Biggs 1988, Fisher & Grimm 1988, Biggs & Close 1989, Grimm & Fisher 1989, Uehlinger 1991, Power 1992, Chapter 2). Many studies have also demonstrated that high resource supply (these results mainly being for the inorganic nutrients nitrogen and phosphorus) tend to stimulate growth rates of some populations and lead to high peak community biomass, and dominance by large celled filamentous taxa in unshaded streams (e.g., Lyford and Gregory 1975, Horner et al. 1983, 1990; Bothwell 1985, 1989, Lowe et al. 1986, Biggs 1990a, Lohman et al. 1991).

However, the interactive effects of disturbance and nutrient supply must be considered if a robust theory based on disturbance and resources is to be developed for periphyton. Biggs (1988), Fisher and Grimm (1988) and Biggs and Close (1989) first addressed this in natural streams. Biggs (1988) reported that disturbance-related

parameters explained 62% of the variance in periphyton ash-free dry mass during summer in 66 New Zealand streams and ion concentration explained a further 15.6%. Fisher and Grimm (1988) found that 67% of the temporal variance in biomass in a Sonoran Desert stream was explained by disturbance, but only an additional 4% by nutrients. In a comprehensive assessment of these interactions, Biggs and Close (1989) reported that 69% of the mean monthly chlorophyll *a* biomass over a year among nine New Zealand streams was explained by nutrient supply, and only 25% by flood disturbance. However, strong collinearity occurred between these two variables suggesting that nutrient supply was influenced, in-part, by flood flow regimes and thus was carrying information relating to both parameters. In Chapter 2, I reported that 86.5% of the variance in mean monthly chlorophyll *a* biomass over a year in a further set of 15 other New Zealand streams was explained by disturbance frequency and nutrient supply. Data from this second study (Tables 1 and 5 of Chapter 2) have been used to place parameter values on the habitat matrix for periphyton (Fig. 6.2) and then mean monthly chlorophyll *a* contours were calculated as a function of disturbance frequency and cellular nitrogen concentrations using linear multiple regression. The contours clearly support the expected gradient in biomass across the habitat matrix as discussed earlier (Fig. 6.1).

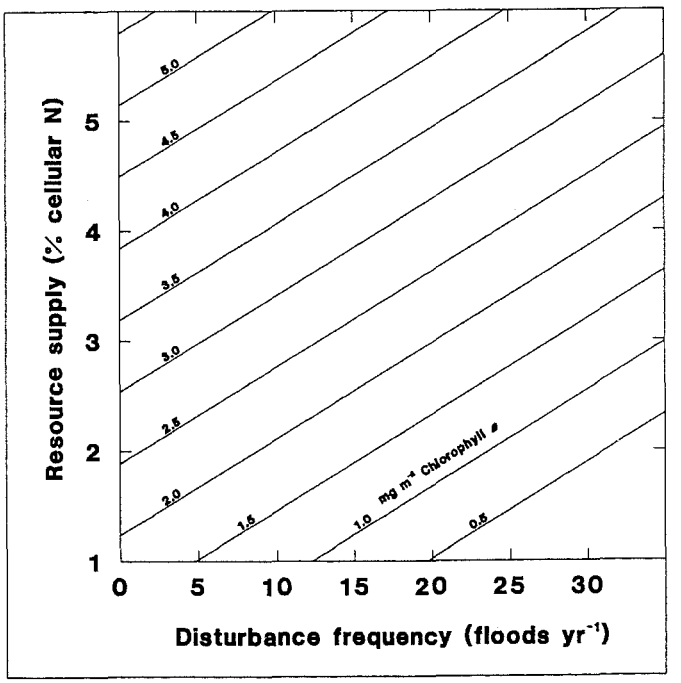


Fig. 6.2: A periphyton habitat matrix with disturbance frequency being quantified as the frequency of velocities exceeding 1 m/s per year and limiting nutrient supply being quantified as cellular nitrogen concentrations. The contours define a gradient in $ln_e$ mean monthly chlorophyll *a* and were developed by regressing chlorophyll *a* on $\%N_c$ and disturbance frequency (r2 = 0.865) (based on data in Chapter 2).

*Provisional allocation of disturbance - nutrient resource supply habitat preferences for some common algal periphyton*

The habitat preferences of 35 periphytic algae have been provisionally allocated into four primary disturbance - nutrient resource supply guilds (Fig. 6.3) based on a range of published and unpublished field and experimental studies. These taxa are all found abundantly, or as dominants, in temperate streams. Their allocation on the habitat matrix reflects where they appear to be most competitive. However, it does not preclude their presence in other cells of the matrix (although they may not dominate there), particularly as components of post-disturbance successions (see later section on community stability). It is important to note that the potential for species replacement as a function of nutrient supply is high so long as disturbance frequency is low. For example, I have identified 22 common taxa that could potentially dominate depending on nutrient supply (i.e., Guilds 1 - 3). However, the potential for species replacement as a function of increasing disturbance frequency is low because the pool of species adapted to persist in high disturbance environments appears to be small. In moderately disturbance prone environments I have identified 11 common taxa that could dominate (i.e., Guilds 4a-c) and only two taxa in the highly disturbance prone environments (i.e., Guild 4d). Thus, in highly disturbed habitats species richness and diversity is expected to be low (this has also been noted for other ecosystems; Crawley 1986). This situation can be hypothesised to be a result of two things. Firstly, few stream periphyton taxa appear to have evolved to exploit very high disturbance environments and, secondly, this may reflect a greater occurrence in nature of low disturbance habitats (but ones which cover a range of nutrient supply regimes).

Four groups of traits are proposed which are hypothesized to control relative competitive success as joint functions of disturbance - nutrient resource supply. These traits are morphology/physiognomy, life history, physiology, and resistance to herbivory. The presence (or absence) of individual traits for each group of taxa was assessed from literature and unpublished data (Table 6.1). These data are summarised in Table 6.2 to qualitatively describe the growth strategy attributes of taxa in each of four guilds of algal species.

It is important to understand that no one trait is likely to confer dominance in particular cells of the habitat matrix. Dominance will be conferred by different combinations of these traits, together with the availability of a pool of propagules.

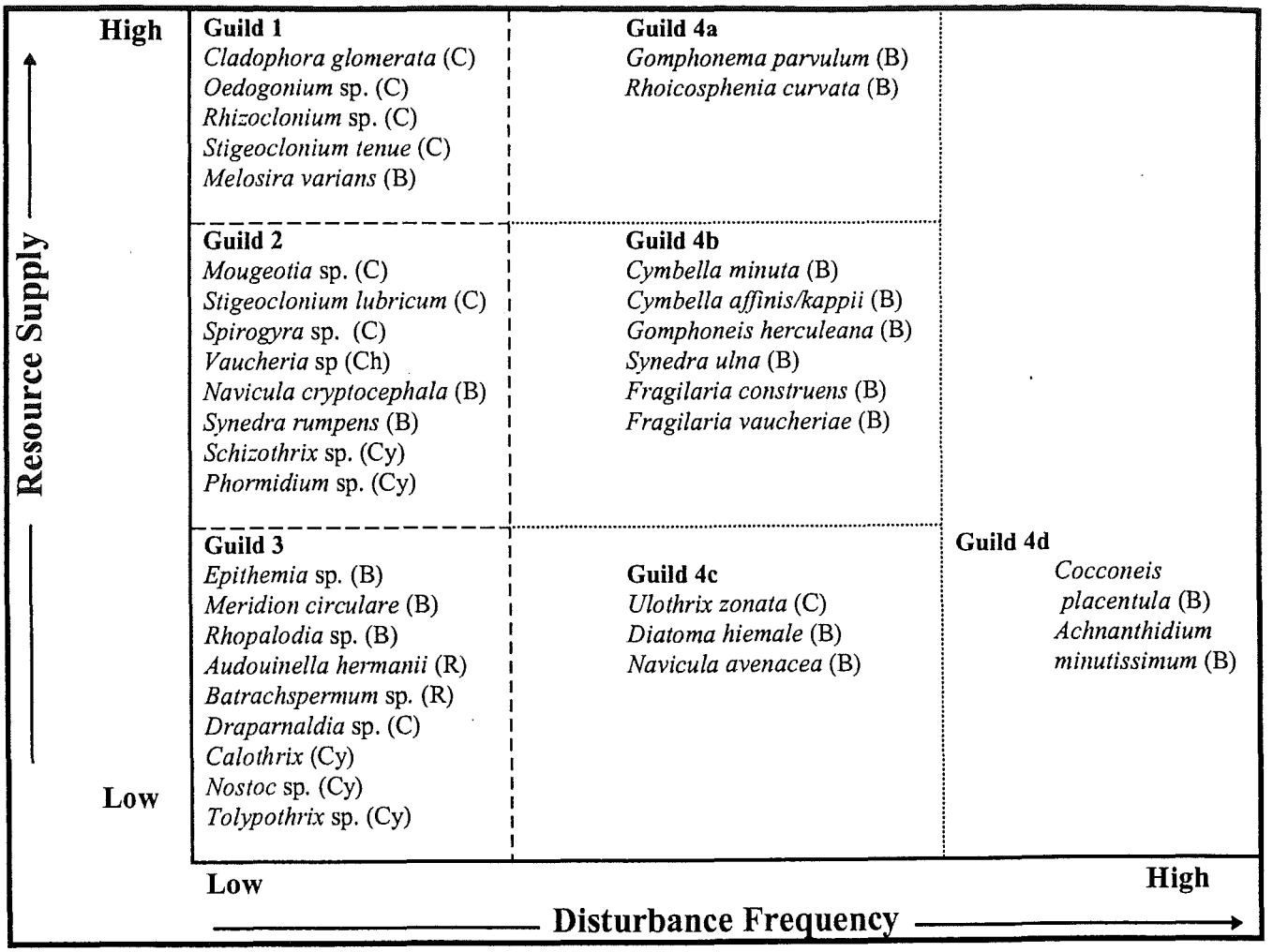


Fig. 6.3: 'Most preferred' location of periphyton taxa on the disturbance - nutrient resource supply habitat matrix assessed from literature sources (B = Bacillariophyta/diatoms, C = Chlorophyta/green algae, Ch = Chrysophyta, Cy = Cyanobacteria, R = Rhodophyta/red algae).

**Guild 1: Taxa favouring low disturbance, high nutrient supply habitats**

Taxa which are successful in this niche in terrestrial ecosystems have been classified as 'competitive' (Grime 1979). Several filamentous green algal species (Chlorophyta) and the filamentous diatom (*Melosira varians*) are members of this guild (Fig. 6.3). These taxa generally have an upright physiognomy (until the filaments extend into flowing waters when they flex), have medium - large cells forming uniseriate, branched or unbranched filaments, and some have thickend cellulose walls that are often colonised by epiphytes (e.g., *Cladophora glomerata* and *Rhizoclonium* sp.) (Prescott 1973) (Table 6.1). These taxa appear to have an inherent demand for high nutrients (particularly nitrogen and phosphorus) as they most commonly dominate periphyton mats, and can reach high peak biomasses in enriched streams during

***Table 6.1 Attributes of taxa in the disturbance - resource supply guilds***

| | **Guild 1** | **Guild 2** |
|---|---|---|
| | *C. glomerata* | *Mougeotia* |
| | *Oedogonium* | *Vaucheria* |
| | *Rhizoclonium* | *Stig. lubricum* |
| | *Stig . tenue* | *Spirogyra* |
| | *Melosira varians* | *N. cryptocephala* |
| | | *S. rumpens* |
| | | *Schizothrix* |
| | | *Phormidium* |
| *1: Community Morphology/Physiognomy* | | |
| Single holdfast cell | some | some |
| Heterotrichous holdfasts (incl. rhizoids) | some | some |
| Mucilage pad holdfasts | no | *Synedra* |
| Stalk holdfasts | no | no |
| Adnate | no | *Synedra* |
| Prostrate | *Stigeoclonium* | yes |
| Cells large | yes | *Spirogyra* |
| Unicellular | no | some |
| Weakly motile | no | no |
| Strongly motile | no | *Navicula* |
| Filamentous - unbranched | some | some |
| Filamentous - branched | some | some |
| Host for epiphytes | some | some |
| Thick mat formation | yes | yes-no |
| Thick mucilage formation | no | no |
| *2: Life History* | | |
| Episodic reproduction/zoosporogenesis | some | some |
| Filam. fragmentation | some | some |
| High immigration potential | no | no |
| *3: Physiology* | | |
| Coarse cellulose walls | some | *Vaucheria ?* |
| High detachment resistance | *Stigeoclonium* | no |
| Light demanding | yes | some |
| N-fixing | no | no |
| High half saturation coeff. | no | no |
| High peak biomass | yes | *Vaucheria* |

***Table 6.1***

| | **Guild 3** | **Guild 4a** |
|---|---|---|
| | *Epithemia*<br>*M. circulare*<br>*Rhopalodia*<br>*Aud. hermanii*<br>*Batrachospermum*<br>*Draparnaldia*<br>*Calothrix*<br>*Nostoc*<br>*Tolypothrix* | *G. parvulum*<br>*R. curvata* |
| *1: Community Morphology/Physiognomy* | | |
| Single holdfast cell | some | no |
| Heterotrichous holdfasts (incl. rhizoids) | some | no |
| Mucilage pad holdfasts | some | yes |
| Stalk holdfasts | no | no |
| Adnate | *Epithemia* | yes |
| Prostrate | no | no |
| Cells large | some | no |
| Unicellular | some | yes |
| Weakly motile | *Epithemia* | yes |
| Strongly motile | no | no |
| Filamentous - unbranched | *Nostoc* | no |
| Filamentous - branched | some | no |
| Host for epiphytes | no | no |
| Thick mat formation | no | no |
| Thick mucilage formation | no | no |
| *2: Life History* | | |
| Episodic reproduction/zoosporogenesis | *Draparneldia* | no |
| Filam. fragmentation | some | no |
| High immigration potential | no | no |
| *3: Physiology* | | |
| Coarse cellulose walls | no | no |
| High detachment resistance | some | ? |
| Light demanding | no | ? |
| N-fixing | many | no |
| High half saturation coeff. | ? | ? |
| High peak biomass | no | no |

*Table 6.1*

| | Guild 4b | Guild 4c |
|---|---|---|
| | *C. affinis/kappii* | *Ulothrix zonata* |
| | *C.minuta* | *Diatoma hiemale* |
| | *F. construens* | *N. avenacea* |
| | *F.vaucheriae* | |
| | *G. herculeana* | |
| | *S. ulna* | |
| *1: Community Morphology/Physiognomy* | | |
| Single holdfast cell | no | *Ulothrix* |
| Heterotrichous holdfasts (incl. rhizoids) | no | *Ulothrix* |
| Mucilage pad holdfasts | yes | some |
| Stalk holdfasts | yes | no |
| Adnate | some | some |
| Prostrate | some | *Navicula* |
| Cells large | *Gomphoneis* | no |
| Unicellular | yes | *Navicula* |
| Weakly motile | no | no |
| Strongly motile | some | *Navicula* |
| Filamentous - unbranched | no | except *Navicula* |
| Filamentous - branched | no | no |
| Host for epiphytes | no | no |
| Thick mat formation | no | yes-no |
| Thick mucilage formation | yes | no |
| *2: Life History* | | |
| Episodic reproduction/zoosporogenesis | no | *Ulothrix* |
| Filam. fragmentation | no | *Diatoma* |
| High immigration potential | yes | yes |
| *3: Physiology* | | |
| Coarse cellulose walls | no | no |
| High detachment resistance | yes | *Ulothrix* |
| Light demanding | no | *Ulothrix* |
| N-fixing | no | no |
| High half saturation coeff. | yes | ? |
| High peak biomass | some | some |

*Table 6.1*

| | **Guild 4d** |
|---|---|
| | *A. minutissimum* |
| | *C. placentula* |
| *1: Community Morphology/Physiognomy* | |
| Single holdfast cell | no |
| Heterotrichous holdfasts (incl. rhizoids) | no |
| Mucilage pad holdfasts | yes |
| Stalk holdfasts | *Achnanthidium* |
| Adnate | yes |
| Prostrate | yes |
| Cells large | no |
| Unicellular | yes |
| Weakly motile | yes |
| Strongly motile | no |
| Filamentous - unbranched | no |
| Filamentous - branched | no |
| Host for epiphytes | no |
| Thick mat formation | no |
| Thick mucilage formation | no |
| *2: Life History* | |
| Episodic reproduction/zoosporogenesis | no |
| Filam. fragmentation | no |
| High immigration potential | yes |
| *3: Physiology* | |
| Coarse cellulose walls | no |
| High detachment resistance | yes |
| Light demanding | no |
| N-fixing | no |
| High half saturation coeff. | yes |
| High peak biomass | no |

prolonged periods of hydrological stability (e.g., Biggs and Price 1987, Biggs 1990, Dodds and Gudder 1992, Chapter 2). *Cladophora* has relatively high nutrient uptake half-saturation constants of 15 - 257 ugP/l and does not tolerate shading (Whitton 1975, Auer and Canale 1982, Lohman and Priscu 1992). Half-saturation constants for *Stigeoclonium tenue* range from 15 to 93 ugP/l (Rosemarin 1982). In terms of its broader ecology, *Cladophora* is well known as a mid-late successional species (Fisher et al. 1982, Dudley and D'Antonio 1991, Power 1992) and it is relatively resistant to grazing (Dodds and Gudder 1992).

Reproductive strategies of taxa in this guild (Table 6.1) are most commonly a combination of episodic zoosporogenesis and filament fragmentation/cell division (Prescott 1973). Zoosporogenesis may be an important mechanism for the dispersal and periodic appearance of some of these taxa, but little is known of factors that promote such events (e.g. for *Cladophora* see Dodds and Gudder 1992).

Modes of attachment and architecture are fundamental to drag and the ability of the community to withstand disturbance (Chapter 3). *Cladophora, Oedogonium, Rhizoclonium* and *Stigeoclonium* all have specialised or heterotrichous holdfast structures (Prescott 1973). This helps these taxa resist drag created by their vertical extension into the flow as mats grow. Through this, these taxa can acclimate to quite high (~0.7 m/s), steady water velocities (B. J. F. Biggs unpub.). *Melosira* does not have specialised holdfast structures and intercellular connections appear to be weak. For all these large filamentous algae, form drag (i.e., the cross-sectional surface area presented directly into the flow) is likely to be far more significant than skin friction and the magnitude of this drag will grow in proportion to the square of the overlying water velocity (Kohel 1982). Thus, communities dominated by such filamentous taxa appear to be particularly prone to hydrological disturbance (e.g., Grimm and Fisher 1989, Uehlinger 1991, Peterson and Stevenson 1992, Chapter 3).

None of the taxa in this guild have been reported as rapid colonists of denuded substrata.

Overall, the distinctive characteristics of taxa in this guild are that their growth requires high levels of nutrients; they appear to be slow or episodic colonizers of denuded substrata; they are erect, architecturally complex filamentous taxa which can harbour epiphytes; they can form high biomass, and they are prone to disturbance by flooding (Table 6.2). Thus, they tend to only dominate enriched habitats which are infrequently disturbed by floods.

**Guild 2: Taxa favouring low disturbance, medium nutrient supply habitats**

The taxa in this guild are a transition group along the nutrient supply gradient and do not appear resistant to flood disturbance. They comprise green algae, diatoms and cyanobacteria (Fig. 6.3). They display a great range in morphological and architectural features. They may be upright or prostrate, have small - medium cell sizes, and include unicellular and filamentous taxa (Table 6.1). They rarely harbour epiphytes.

*Mougeotia, Stigeoclonium lubricum, Spirogyra, Phormidium* and *Synedra rumpens* often dominate periphyton assemblages in streams with medium - low ion concentrations (i.e., 50 - 150 umol/cm conductivity; Biggs and Price 1987, Biggs 1990, Chapter 2, Biggs unpublished). Laboratory studies have demonstrated that when growing together, phosphorus enrichment favours the growth of *Phormidium* over *Mougeotia* (Horner et al. 1990), and half saturation co-efficients of phosphorus of 7 - 25 ug/l have been reported for *Mougeotia - Phormidium* dominated communities (Horner et al. 1983, 1990, Seely et al. 1994). Half saturation co-efficients for *Spirogyra* (as *S. fluviatilis*) are more variable, ranging from 8.7 - 47.2 ug/l depending on the phase of growth and how replete the cells already are in P (Borchardt et al. 1994). These values overlap the lower range, but also go much lower than, those found for *Cladophora* in the high nutrient supply guild (see above).

Taxa such as *Mougeotia, Spirogyra* and *Phormidium* tend to be much slower to colonize and grow in denuded habitats than some of the common diatoms (which may persist through disturbance events, Chapter 3). However, these taxa are faster colonisers than Guild 1 taxa such as *Rhizoclonium* (Power and Stewart 1987, Peterson and Stevenson 1990, 1992). In particular, *Phormidium* does not commonly dominate the substrata until mid-late in the successional cycle (late summer in streams with seasonally defined disturbance regimes; e.g., Jacoby 1987) and in high nutrient environments this taxon may become outcompeted by large filamentous green algae (e.g., Marker 1976, Power 1992; authors' unpublished data.).

The large range in half saturation co-efficients for *Spirogyra* may reflect a high degree of flexiblity in its nutrient capture traits. This flexibility may be indicative of several of the taxa in this guild (e.g., *Stigeoclonium lubricum, Synedra rumpens, Phormidium* sp.) which, individually, can be found dominating communities over a wide range of enrichment regimes in natural streams (Biggs & Price 1987, Biggs 1990, Biggs & Gerbeaux unpublished data). *Stigeoclonium* can increase terminal hair

Table 6.2: Summary traits of taxa in the main cells of the disturbance - resource supply habitat matrix

---

**1: Guild1 - Low Disturbance, High Limiting Resource Supply**
mainly green algae
upright, large celled branched/unbranched filamentous taxa
some with tough cellulose walls and epiphytes
high half saturation constants for nutrient uptake, slow growing
light demanding
forming high peak biomass
reproduction often episodic, also filament fragmentation/mitosis
mainly poorly attached by single holdfast cells

**2: Guild 2 - Low Disturbance, Medium Limiting Resource Supply**
mainly green algae, sometimes diatoms or cyanobacteria
upright and prostrate med. - small cell, unbranched filamentous and unicellular
high half saturation constants for nutrient uptake, slow growing
mod. light demanding
forming medium peak biomass
range in modes of attachment
some reproduce episodically, others by filament fragmention/mitosis

**3: Guild 3 - Low Disturbance, Low Limiting Resource Supply**
mainly diatoms, cyanobacteria and red algae
upright and prostrate, small celled
large variety of forms; unicellular, simple-complex branching, globose
many fix nitrogen
reproduce mainly by filament fragmentation/mitosis
forming low peak biomass
some well attached others not

**4: Guild 4a - Medium Disturbance, High Limiting Resource Supply**
unicellular diatoms
upright, adnate attached by mucilage pads
peak biomass medium - low

**5: Guild 4b - Medium Disturbance, Medium Limiting Resource Supply**
unicellular diatoms, med. - small in size
mainly upright, adnate attached by mucilage pad or stalk
capable of high mucilage production
peak biomass medium - high
high immigration potential
low nutrient half saturation constants

**6: Guild 4c - Medium Disturbance, Low Limiting Resource Supply**
unicellular diatoms and an unbranched filamentous green alga
prostrate and upright with specialized holdfast for filamentous
some motile
capable of some mucilage production
episodic reproduction and filament fragmentation in some
peak biomass potential low - medium
high immigration potential in some

**7: Guild 4d - High Disturbance, Low Limiting Resource Supply**
unicellular diatom, small in size
prostrate or adnate, with mucilage pad and stalked holdfast
tight adhesion
low half saturation constant for nutrient uptake
low peak biomass
high immigration potential

---

formation in response to low phosphorus availability and thereby increase its ability to take up P (Gibson and Whitton 1987). Communities dominated by taxa of this guild may vary considerably in peak biomass, but on average it is intermediate between that found in low and high nutrient supply environments (see Biggs and Price 1987 Fig. 5, Biggs 1990, Chapter 2).

Taxa in Guild 2 have a combination of episodic reproduction and filament fragmentation life history strategies (Table 6.1). In this respect they are similar to Guild 1 taxa. The unicellular diatoms *Navicula cryptocephala* and *Synedra rumpens* predominantly reproduce by mitotic division. The taxa in this guild do not appear to have any unique features to their life-history strategies which could contribute to their competitive superiority in the low disturbance - moderate nutrient supply sector of the habitat matrix.

A wide range of modes of attachment and mechanisms to resist disturbance also occur in this guild (Table 6.1). For example, *Mougeotia, Schizothrix* and *Phormidium* are all filamentous taxa which do not have specialised attachment structures. They generally lie prostrate on substrata with the latter two taxa (both Cyanobacteria) forming compact and cohesive mats of intertwined trichomes bound by mucilage which often does not dissociate easily (Prestcott 1973). In contrast, *Stigeoclonium* and *Spirogyra* are more upright and develop from heterotrichous filaments or holdfast cells. However, as biomass develops in both taxa the attachment device appears to become vulnerable to drag of the overlying filaments. This occurs particularly in *Stigeoclonium* where multiple branching can result in an extensive dendritic structure which is attached solely by a uniseriate 'trunk' from the pseudoparenchymatous basal layer. Finally, the diatoms have two different ways in which they can be attached. *Synedra rumpens* can be prostrate, or quite commonly adnate, with cells forming rosettes attached apically by a small mucilage pad (Lamb and Lowe 1987). Conversely, *Navicula cryptocephala* is a raphed, prostrate diatom which is usually motile.

Because of this wide range of structural characteristics, and the effect of increasing biomass on drag (see discussion under Guild 1), the suceptibility to disturbance by floods of mats dominated by these taxa will vary greatly. For example, young cohesive mats formed by some cyanobacteria such as *Calothrix* and *Schizothrix*, low growing diatom communities, and new growth of filamentous taxa such as *Spirogyra* can be particularly resistant to hydrological scour (Power and Stewart 1987, Peterson et al. 1990, Peterson and Stevenson 1992, Peterson et al. 1994, Chapter 3). However,

mature communities dominated by *Mougeotia, Spirogyra* and *Phormidium* are particularly sensitive to increases in shear stress and physical abrasion (Power and Stewart 1987, Horner et al. 1990, Peterson and Stevenson 1992, Chapter 3). Indeed, in Chapter 3 I report that a 50% loss in biomass of *Melosira varians* and *Spirogyra* dominated communties could occur with a 3-6 fold increase in shear stress whereas a > 70 fold increase in shear stress was required to remove a prostrate diatom community dominated by *Fragilaria* and *Cymbella* species. Initial biomass only had a small effect on the outcome. As with the filamentous taxa, both diatoms of this guild (*Navicula cryptocephala* and *Synedra rumpens*) are also relatively prone to shear stress dislodgement (Peterson and Stevenson 1992, Chapter 3).

Overall, the distinctive characteristics of taxa in Guild 2 are that several have their growth saturated at moderate concentrations of nutrients, they are moderate - slow to colonize and develop in denuded habitats, they are architecturally heterogeneous, they can attain moderate biomasses, and they are usually prone to hydrological disturbances (Table 6.2).

**Guild 3: Taxa favouring low disturbance, low nutrient supply habitats**

This sector of the habitat matrix contains what Grime (1979) termed for terrestrial habitats the 'stress tolerant' taxa. In streams, periphyton belonging to this group include representatives of the green algae, diatoms, red algae and cyanobacteria (Fig. 6.3). They are predominantly filamentous with medium to small cell sizes and simple to complex branching. As with taxa in the other low disturbance guilds (Guilds 1 and 2), these taxa also tend to be erect with potentially high form drag, although the diatoms *Epithemia* and *Rhopalodia* are prostrate while *Meridion* is erect. The cyanobacteria *Calothrix* and *Tolypothrix* form mats of prostrate intertwined filaments embedded in mucilage. These taxa rarely harbour epiphytes (Table 6.1).

Most taxa belonging to this guild reproduce by simple filament fragmentation and/or mitosis. No data are available on their nutrient affinities. However, of note is that over half of the guild are nitrogen fixers (i.e., *Epithemia, Rhopalodia, Nostoc, Tolypothrix* and *Calothrix*), an ability that allows these taxa to tolerate and exploit niches with low concentrations of aqueous phase nitrogen. This facility is almost entirely restricted to this low disturbance, low nutrient supply guild. It is also well established that red algae tolerate very low levels of light and nutrients (e.g., *Audouinella* and *Batrachospermum*) (Sheath and Hambrook 1990). Thus, they grow well in shaded forest streams on very stable substrata. These red algal taxa are also thought to have low growth rates relative to green algae and diatoms (e.g. Hynes

1970) although this does not appear to have been demonstrated empirically. Overall, the taxa making up this guild tend to form low peak biomass.

A variety of holdfast mechanisms in this guild ranging from simple prostrate adhesion (*Epithemia*) to heterotrichy (*Audouinella*) and mats of mucilage (*Tolypothrix* and *Calothrix*) are exhibited by members of this guild. *Draparnaldia* displays a combination of characters. The plants consist of whorled fascicles embedded in copious, soft mucilage. The filaments give rise to rhizoidal branches at the base (Prescott 1973). Accordingly, some of these taxa are firmly attached to the substratum and can be quite resistant to shear stress disturbance (e.g., *Audouinella*; Biggs and Shand 1987). Some cyanobacterial mats (e.g., those dominated by *Calothrix*) have been found to be resistant to gravel abrasion also (Peterson et al. 1994).

Overall, these communities can be characterised as being extremely diverse taxonomically and physically. Through means such as nitrogen fixation and specialised nutrient physiology they are able to tolerate low nutrient conditions, and many also appear to have moderate disturbance resistance (Table 6.2).

**Guild 4: Taxa favouring medium - high disturbance, variable nutrient supply habitats**

This guild incorporates those taxa that are the early colonists of denuded habitats (Fig. 6.3). Overall, they are the opportunistic, "weedy" taxa of periphyton. If there are repeated disturbance events or continuing physical stresses following disturbance (e.g., from constantly high water velocities, physical abrasion or grazing) then this guild will be favoured.

The guild is composed almost entirely of diatoms and the broad persistence of diatoms in disturbed environments has been widely documented (e.g., Grimm and Fisher 1989, Peterson and Stevenson 1992, Chapter 3; however, see Peterson et al. 1994 for an exception). This occurs because many members of the community have high disturbance resistance and rapid post-disturbance immigration (Luttenton and Rada 1987, Robinson and Rushforth 1987, Stevenson 1990, Peterson and Stevenson 1991, 1992, Chapter 3). In natural streams, these taxa can be important components of the periphyton over almost the entire habitat matrix and are the dominant component of early successional seres no matter what the nutrient supply is (Fisher et al. 1982; Peterson and Stevenson 1990, 1992; Biggs 1990, Chapter 2; Biggs unpublished). Once established as dominants in moderate - low nutrient supply

habitats, these taxa may also monopolise some substrata (e.g., Biggs and Gerbeaux 1993, Chapter 5).

While Guild 4 taxa are more habitat generalists than those in Guilds 1 - 3 (and thus can be found as a common component of communities in most habitats, at most times), many of them are stronger competitors in certain cells of the habitat matrix and will tend to be more common or dominate there. Thus, four sub-guilds have been defined for these taxa (Fig. 6.3).

Overall, taxa in this guild have one, or a combination, of three important traits which facilitate their success over such a wide range of disturbance conditions. They have high resistance to removal by hydrological disturbance; high immigration rates; and low half saturation constants for nutrient uptake allowing rapid growth even if nutrient resource supplies are low following disturbance (Table 6.1). The high resistance of *Achnanthidium minutissimum* to removal has been widely demonstrated (e.g., Rounick and Gregory 1981, Luttenton and Rada 1986, Robinson and Rushforth 1987, Colletti et al. 1987, Peterson 1987, Peterson and Stevenson 1990). It adheres strongly to surfaces along its raphe valve (Rosowski et al. 1986) or by means of a short subapical mucilagenous stalk (Roemer et al. 1984). Other taxa in this guild that are also relatively resistant to high shear stress include *Cocconeis placentula, Fragilaria vaucheriae, F. construens, Gomphoneis herculeana, Navicula avenacea, Gomphonema parvulum,* and *Synedra ulna* (Chapter 3). Only *Navicula avenacea* is not strongly attached apically, or by mucilagenous stalks or pads.

The taxa associated with disturbed high nutrient supply environments (*Gomphonema parvulum, Rhoicosphenia curvata)*, and very disturbed low - high nutrient supply environments (*Cocconeis placentula* and *Achnanthidium minutissimum*) are all very commonly found as epiphytes on macroalgae such as *Cladophora* and macrophytes (e.g., Luttenton and Rada 1986, Biggs and Price 1987). When on macrophytes, they can also occur in moderately low nutrient supply habitats, possibly utilizing leaf exudates as a nutrient source (Wetzel 1983).

The only non-diatom taxon in this guild is the uniseriate filamentous green alga *Ulothrix zonata.* It attaches to the substratum via a specialized holdfast cell (Prescott 1973) and has high resistance to increases in shear stress (Chapter 3). It is often seen dominating disturbance-prone mountain streams which have low nutrient supplies (Biggs and Price 1987, Biggs 1990, B.J.F. Biggs unpublished) although it actually

appears to grow better under conditions of moderate to low velocity (e.g., Poff et al. 1990).

One of the most important attributes that contributes to the successful invasion of disturbed substrata by taxa of this guild stems from their relatively small size and ability to divide at least daily. This provides a ready pool of propagules for emigration to new substrata. Indeed, these diatoms appear to have higher immigration rates onto denuded habitats than filamentous green algae or cyanobacteria and are characteristic of early colonisation (e.g., Fisher et al. 1982). Also, a number of studies have shown that prostrate, tightly attached taxa (e.g., monoraphid diatoms) are succeded by apically attached araphid diatoms (these may then be succeded by stalked and filamentous algae, which are best able to compete for resources of nutrients and light at the top of the dense mat; Hudon and Bourget 1981, Hoagland et al. 1982, Stevenson 1984, Oemeke and Burton 1986, Steinman and McIntire 1986, Stevenson and Peterson 1991). Other rapidly colonising diatoms include *Achnanthidium minutissimum* (in higher velocity areas, Stevenson 1983), *Cocconeis placentula, Cymbella* sp., and *Fragilaria vaucheriae* (Stevenson and Peterson 1989).

The ability to capture nutrients and saturate growth at low concentrations should confer some advantage to early successional species to exploit denuded habitats. These same traits may also allow such species to be maintained in communities when nutrient depletion occurs as the three dimensional architecture of the mat grows and climax species begin to dominate. Half saturation coefficients of lotic diatoms appear to be much lower than for green algae. Bothwell (1985) reported values ranging between 0.5 and 7.2 ugP/l for communities that were dominated by diatoms including *Fragilaria vaucheriae* and *Achnanthidium minutissimum.* Having such high nutrient resource capture rates, and the ability to still grow well under conditions of high nutrient supply (i.e., high nutrient concentrations are not inhibitory), enables these taxa to occur over a great range of nutrient resource conditions.

Overall, taxa in this guild can be characterised as being low profile, moderately - strongly attached with rapid immigration potential, rapid rates of cell division and high potential to exploit nutrients at low concentrations (Table 6.2). Through these attributes they are disturbance - resistant and opportunistic.

## III. Grazers: the third dimension of the habitat matrix

It widely recognised that grazing is also an important determinant of stream periphyton biomass and community structure in many situations (Gregory 1983, Steinman 1996). Grazing can significantly reduce biomass and maintain a community dominated by species with disturbance resistance traits (Steinman et al. 1987, Peterson and Stevenson 1992). However, two important questions need to be addressed to integrate the effects of grazing into the habitat matrix of periphyton. First, how does the structure of the herbivore community change along the disturbance gradient of the habitat matrix ? Herbivore density and composition are also functions of disturbance (e.g., Scarsbrook and Townsend 1993, Death 1995) and can be expected to have a strong bearing on the intensity of herbivory on periphyton. Second what rate of periphyton production (reflecting nutrient resource supply) can herbivores consume and thus significantly retard periphyton biomass accrual (i.e., relative degree of periphyton consumption over periphyton production for different invertebrates) ?

*Invertebrate community structure as a function of disturbance*

Disturbance by flooding is an important regulator of invertebrate community structure and (as suggested here for periphyton) is now considered to be one of the fundamental axes of the invertebrate habitat template (Hildrew and Townsend 1988, Minshall 1988, Resh et al. 1988, Townsend 1988, Poff and Ward 1989, Poff 1992, Scarsbrook and Townsend 1994, Townsend and Hildrew 1995). Shifts in community structure along a disturbance frequency gradient can be interpreted as trade-offs between size/drag, attachment strength, mobility, and life history traits (e.g., univolitine vs. multivolitine). Large, weakly attached and weakly mobile grazers such as snails (and certain large caddis larvae) appear to be particularly prone to dislodgement by even moderate increases in water velocity. For example, *Dicosmoecus gilvipes* cannot graze in locations of high current velocity (Hart 1981), so much of its activity is concentrated in pools and along stream margins. Such large and weakly mobile taxa tend to be restricted to streams that are not prone to high velocity flood events (e.g., Scarsbrook & Townsend 1993, Death 1995). There are some exceptions, however. The snail *Elimia clavaeformis* has a stout shell and appears to be somewhat resistant to floods. Hill (1992) reported that densities of this snail in a Tennesse stream did not decline significantly after a flood with a 40 fold increase in discharge.

High gradient and highly unstable environments select for taxa which are streamlined to withstand high shear stress, are highly mobile (which is likely to aid their ability to seek refuge from potentially disturbing events), have multivolitine life histories and high immigration potential ensuring rapid recolonization of denuded areas (Hildrew and Townsend 1987, Townsend and Hildrew 1994). In such streams, snails and large-weakly mobile caddisflies are likely to be relatively less abundant or absent, and highly mobile 'weedy' herbivores such as mayflies more abundant (e.g., Hawkins and Furnish 1987, Quinn and Hickey 1990, Scarsbrook and Townsend 1994, Death 1995).

Between these two extremes are communities dominanted by, or with an abundance of, the sessile - weakly mobile taxa (Hildrew and Townsend 1987). These can successfully exploit temporally stable and/or patchy habitats and are often composed of collector-browser caddis larvae (e.g., some hydrobiosidae in New Zealand streams; Quinn and Hickey 1990, Jowett and Duncan 1990). However, mobile generalists can still be abundant. Indeed, across the gradient from high to low disturbance, 'weedy' generalists often remain abundant and are joined by less disturbance - resistant taxa which can come to dominate the community (Townsend and Hildrew 1994, Death 1995). This scenario is analogous to that of the ubiquitous, disturbance - tolerant, diatoms of the Guild 4 periphyton which are common across the whole disturbance - nutrient resource supply gradients, but only become dominant where their larger competitors are selected against by increasing levels of disturbance.

*Herbivore consumption vs. periphyton production*

When periphyton biomass is low, some grazers can track changes in its productivity and this can result in localised increases in numerical abundance and growth rate of the herbivores (e.g., McAuliffe 1984, Richards and Minshall 1988, Lamberti et al. 1989, Hill 1992, Hill et al. 1992, Biggs and Lowe 1994). However, complicating this is the finding that particularly active grazing may result in a reduction in periphyton biomass (e.g. Lamberti and Resh 1981, McAuliffe 1984, Hill et al. 1992). Food may become limiting to invertebrates under these conditions (e.g., Hart 1985, Hill and Knight 1987, Hill 1992, Hill et al. 1992, Lamberti et al. 1989). Conversely, where nutrient resource supplies for periphyton are high and associated periphyton growth rates are also high, the production of organic matter may progressively exceed losses to the grazers. Thus, whether herbivores can successfully depress the accumulation of periphyton biomass is very much dependent on the interaction between the ability of the herbivores to remove newly synthesized organic matter (a function of the density and type of herbivores present) and the rate of organic matter production. Grazing activity can potentially balance periphyton production in physically stable

systems (Steinman et al. 1991). However, fluctuations in controlling resources such as light and nutrients can allow periphyton production to exceed consumption in the short run (e.g. after stream disturbance, in early spring) because of the fast recruitment and doubling times of periphyton (Power 1992). For example, Lamberti et al. (1989) found that > 90% of algal biomass was consumed by *Juga silicula* densities of 250/$m^2$ when periphyton production was low, whereas < 5% was consumed when primary production was high. However, even when periphyton production was high grazing slowed the accrual of biomass and thus maintained (at least temporarily) algal assemblages at an early successional stage.

In general, mayflies appear to have considerably less ability to control periphyton (particularly at higher rates of periphyton production) than caddisflies, and most studies suggest that snails are the most effective herbivores at denuding substrata of periphyton. McAuliffe (1984) found that chlorophyll *a* was 2 fold higher on substrates where larvae of the caddis *Glossosoma* were excluded, but mayflies were present. Hill (1992) reported from a stream survey (in south-eastern USA) that periphyton AFDM was 3 fold higher in streams lacking the snail *Elimia clavaeformis* (but containing caddisflies such as *Neophylax*). Winterbourn and Fegley (1989) and Biggs and Lowe (1994) reported that periphyton chlorophyll *a* on artificial substrata in some New Zealand streams was 4 - 13 times higher where macro-grazers (predominantly the snail *Potamopyrgus antipodarum*) were excluded, but onto which drifting grazers such as mayflies and chironomids had access. The very large cased-caddis *Dicosmoecus gilvipes* is a particularly voracious herbivore in streams of the US Pacific Northwest (e.g., Lamberti et al. 1987) and may be able to control periphyton when production levels are high. Jacoby (1985) reported from a low nutrient supply river in Washington that *D. gilvipes* ingested approximately 8 times more periphyton per mg body weight than a mayfly *Nixe rosea*. Hawkins and Furnish (1987) speculated that the snail *Juga silicula* is a competitive dominant (depressing densities of other invertebrates) in streams of the western United States through a process of exploitative competition for food and interference.

As rates of nutrient supply and periphyton productivity increase, there is also a change toward dominance of large-celled filamentous algae (Guild 1, see earlier discussion). This affects the grazing success of herbivores as well. For example, *Orthocladius rivulorum* and *Baetis lapponicus* may not consume filamentous algae (Peterson et al. 1993) and Hill (1992) reported that the snail *Elimia calvaeformis* and caddis *Neophylax etnieri* avoided *Cladophora* filaments, but consumed other filamentous algae such as *Phormidium* and *Stigeoclonium* and a range of adnate

diatoms (esp. *Rhoicosphenia*) which occupy the low disturbance, moderate nutrient supply guild of the habitat matrix. Further, at low herbivore densities, spatial patchiness in feeding may allow some periphytic algae, such as *Stigeoclonium*, to reach a size that is less vulnerable to grazing (Steinman et al. 1987). In contrast, larvae of the caddisflies *Dicosmoecus gilvipes* and *Helicopsyche borealis*, and the crayfish *Orconecties*, are known to graze *Cladophora* (Hart 1981, Vaughn 1986, Walton et al. 1994, T. Keller pers. comm.).

Based on a survey of a large number of highly enriched New Zealand streams during summer low flow, Welch et al. (1992) suggested that grazers (such as the cased caddis *Pycnocentrodes aeris*, the mayflies *Deleatidium* spp., the elmid *Hydora* sp. and the snail *Potamopyrgus antipodarum*) probably need to be at densities of > 3,000/$m^2$ to significantly reduce the accrual of periphyton in enriched habitats. If there is periodic disturbance which reduces snail (and perhaps caddis) populations, then there may be windows of opportunity when periphyton biomass can accrue unchecked and proliferations develop (e.g., Power 1992).

*Integration of grazing with disturbance and nutrient supply effects on periphyton*

In summary, most snails (and some large caddis larvae) are less resistant to flood disturbance than the mobile and sessile caddis larvae, which in turn are less resistant than highly mobile mayfly taxa. This sequence appears to be maintained by (and is probably related to) the relative consumptive capacities of these invertebrate groups. The snails appear able to cope with (and control) much higher rates of periphyton production than most caddis larvae (some like *Dicosmoescus gilvipes* being exceptions), which in turn can control much higher rates of production than mayflies. It is likely that these disturbance resistance - herbivory capacity traits represent evolutionary specializations to optimize niche exploitation since flood frequency and nutrient resource supply (controlling rates of periphyton production and biomass accrual) are not independent (Biggs and Close 1989, Chapter 2). The mechanism leading to this is the greater catchment flushing of mineralised nutrients that occurs in areas of high rainfall resulting in inverse relationships between ion concentrations in streams and specific yield (e.g., Close & Davies-Colley 1990). Thus, habitats subject to very frequent flood events tend to have low nutrient supplies, low periphyton biomass and be dominated by mayflies that can effectively use much of the algae produced as a food source. Conversely, habitats with low flood frequencies tend to be more enriched (Close and Davies-Colley 1990, Grimm and Fisher 1992) (but may range down to low levels of enrichment depending on the source of the waters; B. J. Biggs unpublished data), periphyton production is generally much higher and

dominated by large celled taxa (Guild 1, Fig. 6.3), and snails can consume large quantities of the periphyton production. Between these two extremes occur habitats with intermediate levels of disturbance and enrichment where communities often dominated by caddisflies (and also include abundant mayflies) can efficiently harvest (and possibly control) intermediate levels of periphyton production. These relationships are overlayed on the disturbance - nutrient availability matrix in Fig. 6.4.

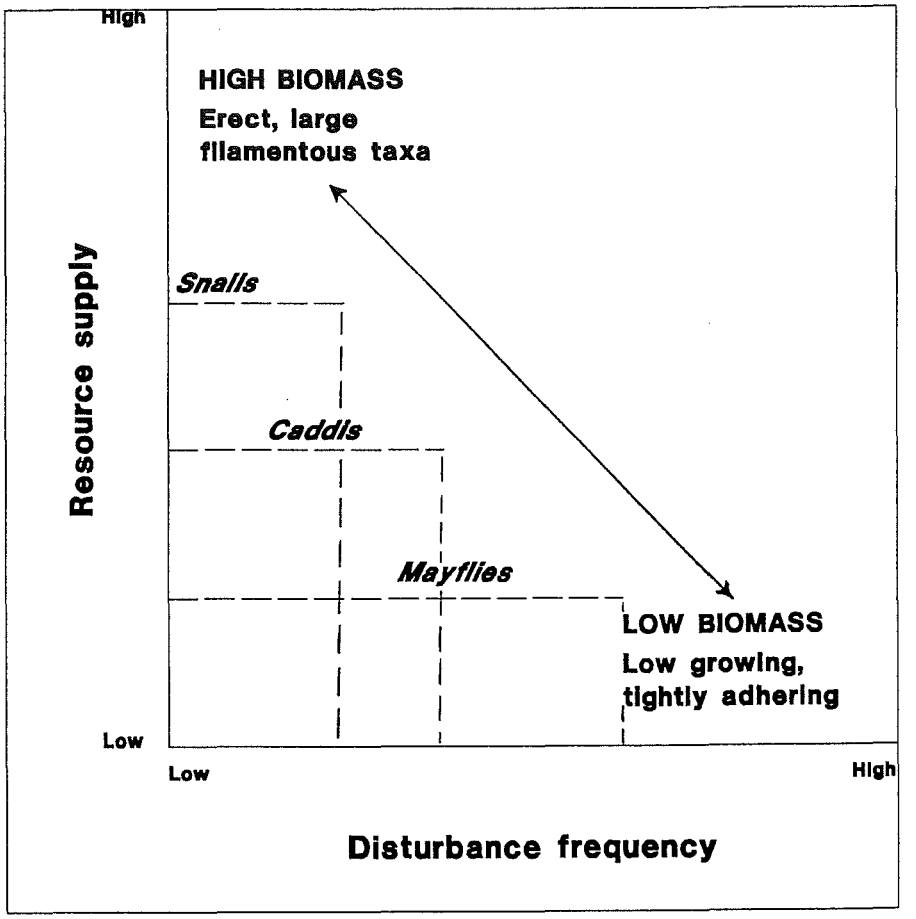


Fig. 6.4: Summary disturbance - resource supply - grazer conceptual model for the control of periphyton development in temperate stream ecosystems. High biomass periphyton communities dominated by erect, large celled filamentous taxa are depicted to dominate in low disturbance - high nutrient supply habitats whereas low biomass communities dominated by low growing, tightly adhering taxa which are resistant to disturbance are depicted to dominate high disturbance - low nutrient supply habitats. High densities of snails can occur in habitats with infrequent flood disturbances and these may exert a significant control on periphyton biomass accrual where nutrient resource supply is low - moderately high. Conversely, mayflies can tolerate much higher levels of disturbance, but will only exert a significant control on periphyton biomass accrual where nutrient resource supply is medium - low. Caddis larvae are depicted to be important controllers of periphyton in the habitats with intermediate levels of disturbance and nutrient resource supply.

## IV. Periphyton community stability and succession

It is important to recognise that the habitat matrix encapsulates both spatial and temporal dimensions. Communities change as a function of time since the last disturbance and temporal variations in nutrient resource supply. In streams with a low frequency of disturbance (e.g., two or three times a season) community dominance is expected to follow through a successional trajectory after the disturbance. It will commence immediately following the disturbance with Guild 4 taxa (in the lower right sector of the habitat matrix) and as the colonisation progresses taxa from Guilds 4b or 4c (depending on nutrient resource supply) will become more abundant (Fig. 6.5). The 'climax' or 'peak biomass' community may ultimately be composed of taxa in Guilds 1, 2 or 3 depending on nutrient resource supply. Further shifts may occur (toward taxa in Guild 3 which are tolerant of low nutrient resource supply) if nutrient resource depletion sets in for environments previously dominated by Guilds 1 and 2 taxa. Indeed, if autogenic sloughing occurs and grazer abundance increases greatly, then dominance in the more resource stressed environments may shift back to taxa with high disturbance/grazer resistance. Conversely, in streams that are subjected to repeated disturbances, communities will remain in the early successional stage (e.g., Luttenton and Rada 1987, Robinson and Rushforth 1988).

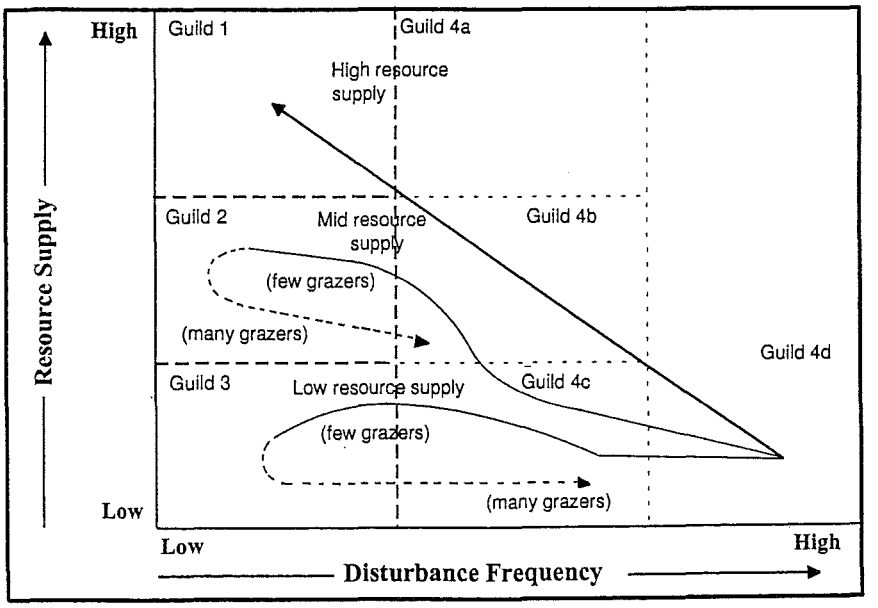


Fig. 6.5: Hypothetical successional trajectories of periphyton communities following intensive flood disturbance in habitats with high nutrient supply (upper trajectory line), moderate nutrient supply (middle line), and low nutrient supply (lower line). It is hypothesised that if periods of inter-disturbance stability are sufficiently long, then invertebrate grazer populations could build up and cause periphyton community structure to change back toward Guild 4b (moderate nutrient supply) or Guilds 4c and 4d (low nutrient supply).

## V. Discussion

I have proposed a concept by which differences and similarities in periphyton structure and function among temperate streams can be understood (and perhaps predicted). The concept is based on the assumption that the physical environment can be partitioned into unique combinations of disturbance frequency and limiting resource supply to form a "habitat matrix". I suggest that different periphyton taxa have evolved specialised traits to enable them to exploit one, or several, sectors of this matrix and shifts in the degree of either (or both) the disturbance frequency or nutrient resource supply can result in a shift in community dominance. Grazing by invertebrates can also be influential in habitats with moderate - low frequencies of disturbance and moderate to low nutrient supplies. Of these three main habitat parameters, I view disturbance frequency by flooding as the primary axis because it is the only truely independent variable. While it can directly affect the periphyton community (through sloughing and abrasion) it also has important effects on nutrient supply, grazer type and grazer abundance, factors that subsequently influence the structure and biomass of the periphyton.

To test this concept more widely it will be necessary to quantify disturbance frequency and nutrient supply in a biologically meaningful way. In the past, disturbance frequency and intensity have rarely been quantified in a physically relevant way which will then allow comparisons among stream systems. Similarly, the rate of limiting resource supply is usually not measured in a meaningful way. Most commonly it is done using dissolved nutrient concentrations in the overlying waters. However, these are often poor indicators of longer-term nutrient supply because of the effects that periphyton have in lowering concentrations during the growth cycle (see discussion in Chapter 2). An approach which I would advocate for future studies, and to enable better quantification of the habitat matrix, is to measure average cellular nutrient quotas over the growing cycle or during the whole of a year (Biggs and Close 1989, Biggs 1990, Humphrey and Stevenson 1992, Chapter 2). This will provide an indication of the historical nutrient supply which has led to the recorded biomass at the time of sampling, something that dissolved inorganic nutrient concentrations do not necessarily do. To quantify disturbance frequency, I advocate the measurement of average sampling site velocities over a range of flows so that velocity rating curves and velocity variations can be calculated over time using the flow record. It is then possible to set criteria such as flows exceeding a given velocity (Chapter 2) and/or determine when bed movement is likely to occur (Poff 1992) to quantify both disturbance frequency and intensity.

This synthesis of recently delineated patterns in periphyton development and distribution into the disturbance - resource supply - grazer concept represents a further contribution to understanding the structure and functioning of stream ecosystems. With such concepts we should be able to understand differences and similarities in systems among different regions and countries. When sufficient understanding has developed as to what degree of perturbation in velocity constitutes a disturbance, and using a quantitative relationship between landuse/geology and limiting resource supply (see Chapter 2, Fig. 2.5), it should be possible to classify streams (and even whole regions) as periphyton habitat in terms of their location on the disturbance - resource supply habitat matrix. By reference to Figs 6.2 and 6.3 it then becomes possible to predict the mean periphyton biomass and species guilds that are most likely to dominate. Such an approach has the potential to contribute greatly to developing an understanding of functional linkages between land and water ecotones, as well as in developing a functional geography of running water ecosystems.

## VI. Summary

The aim of this chapter was to take the results from the previous chapters, integrate them with other studies, and develop a conceptual model of periphyton development with disturbance as the primary axis in order to explain periphyton development among streams and regions. It is hypothesised that different periphyton taxa have evolved to exploit niches partially defined by different combinations of disturbance and nutrient resource supply. It is suggested that high average periphyton biomass is only possible where flood frequency is low and nutrient supply is high. Conversely, a low average biomass will always occur in habitats where flood frequency is high, no matter what the nutrient levels are. Grazing can exert a significant, third order, pressure on biomass development in habitats where flood frequency is moderate - low and nutrient resource supply is moderate - low. Four guilds of taxa which can exploit the different niches on the habitat matrix are proposed. The low disturbance - high nutrient supply guild is composed of erect, large celled filamentous green algae which have high half-saturation coefficients for nutrient uptake and form high peak biomass; the low disturbance - low nutrient supply guild is composed of both unicellular and filamentous taxa (cyanobacteria, green algae, red algae and diatoms) which are generally prostrate, often form copious mucilage and may be nitrogen fixers; the moderate and high disturbance area of the matrix (regardless of nutrient resource supply) is dominated by a guild composed of low growing, tightly adhering diatoms

with high immigration potentials and low half saturation coefficients for nutrient uptake. The effect of grazing invertebrates on the periphyton is variable depending on disturbance frequency, level of nutrient supply and biomass of the animals. A population of snails with moderate - high biomass can exert significant control of the periphyton in habitats with a moderate - low frequency of disturbance, but low - high nutrient supply. A community/population of mayflies with a high biomass can exert significant control in habitats which have a low - high frequency of disturbances and low nutrient supply. Caddis larvae can be important controllers in a disturbance - nutrient supply niche between snails and mayflies. It is suggested that this concept could form the basis for classifying streams as habitat for periphyton based on streamflow records and landuse/geology data.

## VII. References

Auer M.T. & Canale R.P. (1982) Ecological studies and mathematical modelling of *Cladophora* in Lake Huron. 3. The dependence of growth rates on internal phosphorus pool size. *Journal of Great Lakes Research*, **8**, 93-99.

Biggs B.J.F. (1988) Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1405-1411.

Biggs B.J. (1990) Periphyton communities and their environments in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 367-386.

Biggs B.J.F. (1990) Use of relative specific growth rates of periphytic diatoms to assess enrichment of a stream. *New Zealand Journal of Marine and Freshwater Research*, **24**, 9-18.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs B.J.F. & Gerbeaux P. (1993) Periphyton development in relation to macro-scale (geology) and micro-scale (velocity) limiters in two gravel-bed rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **27**, 39-53.

Biggs B.J.F. & Lowe R.L. (1994) Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *New Zealand Journal of Marine and Freshwater Research*, **28**, 119-134.

Biggs B.J.F. & Price G.M. (1987) A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **21**, 175-191.

Biggs B.J.F. & Shand B.I. (1987) *Biological communities and their potential effects of power developments in the Lower Clutha River, Otago*. Ministry of Works and Development. 127p.

Borchardt M.A., Hoffmann J.P. & Cook P.W. (1994) Phosphorus uptake kinetics of *Spirogyra fluviatilis* (Charophyceae) in flowing water. *Journal of Phycology*, **30**, 403-417.

Bothwell M.L. (1985) Phosphorus limitation of lotic periphyton growth rates: an intersite comparison using continuous-flow troughs (Thompsen River system: British Columbia). *Limnology and Oceanography*, **30**, 527-542.

Bothwell M.L. (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1293-1301.

Close M.E. & Davies-Colley R.J. (1990) Baseflow water chemistry in New Zealand rivers. 2. Influence of environmental factors. *New Zealand Journal of Marine and Freshwater Research*, **24**, 343-356.

Colletti P.J., Blinn D.W., Pickart A. & Wagner V.T. (1987) Influence of different densities of the mayfly grazer *Heptagenia criddlei* on lotic diatom communities. *Journal of the North American Benthological Society*, **6**, 270-280.

Crawley M.J. (1986) *Plant Ecology*. 496pp. Blackwell Scientific Publications.

Death R.G. (1995) Spatial patterns in benthic invertebrate community structure: products of habitat stability or are they habitat specific ? *Freshwater Biology*, **33**, 455-467.

Dodds W.K. & Gudder D.A. (1992) The ecology of *Cladophora.* Journal of Phycology, *28, 415-427.*

Douglas B. (1958) The ecology of the attached diatoms and other algae in a stony stream. *Journal of Ecology*, **46**, 295-322.

Dudley T.L. & D'Antonio C.M. (1991) The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology*, **72**, 297-309.

Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monograph*, **52**, 93-110.

Fisher S.G. & Grimm N.B. (1988) Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1183-1190.

Gibson M.T. & Whitton B.A. (1987) Hairs, phosphatase activity and environmental chemistry in *Stigeoclonium, Chaetophora* and *Draparnaldia* (Chaetophorales). *British Phycological Journal*, **22**, 11-22.

Goldsborough L.G. & Robinson G.C.G. (1986) Changes in periphytic algal community structure as a consequence of short term herbicide exposure. *Hydrobiologia*, **139**, 177-192.

Gregory S.V. (1983) Plant - herbivore interactions within stream populations and communities. *Stream ecology: application and testing of general ecological theory* (Eds. J.R. Barnes & G.W. Minshall), pp. 157-189. Stream ecology: application and testing of general ecological theory, Plenum.

Grime J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons. p.

Grime J.P., Rincon E.R. & Wickerson B.E. (1990) Bryophytes and plant strategy theory. *Botanical Journal of the Linnean Society*, **104**, 175-186.

Grimm N.B. (1987) Nitrogen dynamics during succession in a desert stream. *Ecology*, **68**, 1157-1170.

Grimm N.B. & Fisher S.G. (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, **8**, 292-307.

Grimm N.B. & Fisher S.G. (1992) Responses of arid-land streams to changing climate. *Global Climate Change and Freshwater Ecosystems* (Eds. P. Firth & S.G. Fisher), pp. 211-233. Global Climate Change and Freshwater Ecosystems, Springer-Verlag.

Hart D.D. (1981) Foraging and resource patchiness: field experiments with a grazing stream insect. *Oikos*, **37**, 46-52.

Hart D.D. (1985) Causes and consequences of territoriality in a grazing stream insect. *Ecology*, **66**, 404-414.

Hawkins C.P. & Furnish J.K. (1987) Are snails impoartant competitors in stream ecosystems? *Oikos*, **49**, 209-220.

Hildrew A.G. & Townsend C.R. (1987) Organization in freshwater benthic communities. *Organisation of Communities Past and Present* (Eds. J.H.R. Gee & P.S. Giller), pp. 347-371. Organisation of Communities Past and Present, Blackwell Scientific Publications.

Hill W.R. (1992) Food limitation and interspecific competition in snail-dominated streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1257-1267.

Hill W.R. & Knight A.W. (1987) Experimental analysis of the grazing interaction betwen a mayfly and stream algae. *Ecology*, **68**, 1955-1965.

Hill W.R., Weber S.C. & Stewart A.J. (1992) Food limitation of two lotic grazers: quantity, quality, and size-specificity. *Journal of the North American Benthological Society*, **11**, 420-432.

Hoagland K.D., Roemer S.C. & Rosowski J.R. (1982) Colonization and community structure of two periphyton assemblages, with emphasis on diatoms (Bacillariophyceae). *American Journal of Botany*, **69**, 449-457.

Horner R.R., Welch E.B., Seeley M.R. & Jacoby J.M. (1990) Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology*, **24**, 215-232.

Horner R.R., Welch E.B. & Veenstra R.B. (1983) Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. *Periphyton of Freshwater Ecosystems* (Ed. R.G. Wetzel), pp. 121-134. Periphyton of Freshwater Ecosystems, Junk.

Hudon C. & Bourget E. (1981) Initial colonization of artificial substrate: community development and structure studied by scanning electron microscopy. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1371-1384.

Humphrey K.P. & Stevenson R.J. (1992) Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates. *Journal of the North American Benthological Society*, **11**, 37-48.

Hynes H.B.N. (1970) *The Ecology of Running Waters*. University of Toronto Press.

Jacoby J.M. (1985) Grazing effects on periphyton by *Theodoxus fluviatilis* (Gastropoda) in a lowland stream. *Journal of Freshwater Ecology*, **3**, 265-274.

Jacoby J.M. (1987) Alterations in periphyton characteristics due to grazing in a Cascade foothills stream. *Freshwater Biology*, **18**, 495-508.

Jowett I.G. & Duncan M.J. (1990) Flow variability in New Zealand rivers and its relationship to instream habitat and biota. *New Zealand Journal of Marine and Freshwater Research*, **24**, 305-318.

Lamberti G.A., Ashkenas L.R., Gregory S.V. & Seinman A.D. (1987) Effects of three herbivores on periphyton communities in laboratory streams. *Journal of the North American Benthological Society*, **6**, 92-104.

Lamberti G.A., Gregory S.V., Ashkenas L.R., Steinman A.D. & McIntire C.D. (1989) Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology*, **70**, 1840-1856.

Lamberti G.A. & Resh V.H. (1983) Stream periphyton and insect herbivores; experimental study of grazing by a caddisfly population. *Ecology*, **64**, 1124-1135.

Lohman K., Jones J.R. & Perkins B.D. (1992) Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1198-1205.

Lohman K. & Priscu J.C. (1992) Physiological indicators of nutrient deficiency in *Cladophora* (Chlorophyta) in the Clark Fork of the Columbia River, Montana. *Journal of Phycology*, **28**, 443-448.

Lowe R.L., Golladay S.W. & Webster J.R. (1986) Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *Journal of the North American Benthological Society*, **5**, 221-229.

Luttenton M.R. & Rada R.G. (1986) Effects of disturbance on epiphytic community architecture. *Journal of Phycology*, **22**, 320-326.

Lyford J.H. Jr. & Gregory S.V. (1975) The dynamics and structure of periphyton communities in three Cascade Mountain streams. *Verhandlungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **18**, 1610-1616.

Marker A.F.H. (1976) The benthic algae of some streams in southern England. *Journal of Ecology*, **64**, 343-358.

McAuliffe J.R. (1984) Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. *Oikos*, **42**, 327-333.

McCormick P.V. & Stevenson R.J. (1991) Mechanisms of benthic algal succession in lotic environments. *Ecology*, **72**, 1835-1848.

McShaffrey D. & McCafferty W.P. (1991) Ecological association of the mayfly *Ephemerella needhami* (Ephemeroptera: Ephemerellidae) and the green alga *Cladophora glomerata* (Chlorophyta: Cladophoraceae). *Journal of Freshwater Ecology*, **6**, 383-394.

Minshall G.W. (1988) Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society*, **7**, 263-288.

Oemke M.P. & Burton T.M. (1986) Diatom colonization dynamics in a lotic system. *Hydrobiologia*, **139**, 153-166.

Peterson B., Fry B., Deegan L. & Hershey A. (1993) The trophic significance of epilithic algal production in a fertilized tundra river ecosystem. *Limnology and Oceanography*, **38**, 872-878.

Peterson C.G. (1987) Gut passage and insect grazer selectivity of lotic diatoms. *Freshwater Biology*, **18**, 455-460.

Peterson C.G. & Grimm N.B. (1992) Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem. *Journal of the North American Benthological Society*, **11**, 20-36.

Peterson C.G., Hoagland K.D. & Stevenson R.J. (1990) Timing of wave disturbance and the resistance and recovery of a freshwater epilithic microalgal community. *Journal of the North American Benthological Society*, **9**, 54-67.

Peterson C.G. & Stevenson R.J. (1990) Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Botany*, **68**, 2092-2102.

Peterson C.G., Weibel A.C., Grimm N.B. & Fisher S.G. (1994) Mechanisms of benthic algal recovery followinf spates: comparison of simulated and natural events. *Oecologia*, **98**, 280-290.

Peterson E.G. & Stevenson R.J. (1992) Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*, **73**, 1445-1461.

Poff N.L. (1992) Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society*, **11**, 86-92.

Poff N.L. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805-1818.

Power M.E. (1992) Hydrological and trophic controls of seasonal algal blooms in northern California rivers. *Archiv fur Hydrobiologie*, **125**, 375-410.

Power M.E. & Stewart A.J. (1987) Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist*, **117**, 333-345.

Prescott G.S. (1973) *Algae of the Western Great Lakes areas*. Wm C Brown. 977p.

Quinn J.M. & Hickey C.W. (1990) Magnitude of effects of substrate particle size, recent flooding and catchment development on benthic invertebrate communities in

88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 411-427.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Hiram W.L., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance instream ecology. *Journal of the North American Benthological Society*, **7**, 433-455.

Richards C. & Minshall G.W. (1988) The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. *Journal of the North American Benthological Society*, **7**, 77-86.

Robinson C.T. & Rushforth S.R. (1987) Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiologia*, **154**, 49-59.

Roemer S.C., Hoagland K.D. & Rosowski R.J. (1984) Development of a freshwater periphyton community as influenced by diatom mucilages. *Canadian Journal of Botany*, **62**, 1799-1813.

Rosemarin A.S. (1982) Phosphorus nutrition of two potentially competing filamentous algae, *Cladophora glomerata* (L.) Kutz. and *Stigeoclonium tenue* (Agardh) Kutz from lake Ontario. *Journal of Great Lakes Research*, **8**, 66-72.

Rosowski J.R., Roemer S.C., Palmer J. & Hoagland K.D. (1986) Extracellular association and adaptive significance of the bas-relief mucilage pad of *Achnanthes lanceolata* (Bacillariophyceae). *Diatom Research*, **1**, 113-129.

Rounick J.S. & Gregory S.V. (1981) Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. *Hydrobiologia*, **83**, 197-205.

Scarsbrook M.R. & Townsend C.R. (1993) Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Scrimgeour G.J., Davidson R.J. & Davidson J.M. (1988) Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable,

braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, **22**, 337-344.

Scrimgeour G.J. & Winterbourn M.J. (1989) Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia*, **171**, 33-44.

Sheath R.G. & Hambrook J.A. (1990) Freshwater Ecology. *Biology of the Red Algae* (Eds. K.M. Cole & R.G. Sheath), pp. 423-453. Biology of the Red Algae, Cambridge University Press.

Southwood T.R.E. (1977) Habitat, the templet for ecological strategies? Presidential address to the British Ecological Society, 5 January 1977. *Journal of Animal Ecology*, **46**, 337-365.

Southwood T.R.E. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3-18.

Steinman A.D. (1991) Effects of herbivore size and hunger level on periphyton communities. *Journal of Phycology*, **27**, 54-59.

Steinman A.D. (in press) Grazers. *Algal Ecology: Benthic habitats in freshwaters* (Eds. R.J. Stevenson, M.L. Bothwell & R.L. Lowe), . Algal Ecology: Benthic habitats in freshwaters, Academic Press.

Steinman A.D. & McIntire C.D. (1986) Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. *Journal of Phycology*, **22**, 352-361.

Steinman A.D., McIntire C.D., Gregory S.V., Lamberti G.A. & Ashkenas L.R. (1987) Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. *Journal of the North American Benthological Society*, **6**, 175-188.

Steinman A.D., Mulholland P.J. & Kirschitel D.B. (1991) Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure and P uptake in lotic periphyton communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1951-1959.

Stevenson R.J. (1983) Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. *Ecology*, **64**, 1514-1524.

Stevenson R.J. (1984) How currents on different sides of substrates in streams affect mechanisms of benthic algal accumulation. *Internationale Revue der gesamten Hydrobiologie*, **69**, 241-262.

Stevenson R.J. (1990) Benthic algal community dynamics in a stream during and after a spate. *Journal of the North American Benthological Society*, **9**, 277-288.

Stevenson R.J. & Peterson C.G. (1989) Variation in benthic diatom (*Bacillariophyceae*) immigration with habitat characteristics and cell morphology. *Journal of Phycology*, **25**, 120-129.

Stevenson R.J. & Peterson C.G. (1991) Emigration and immigration can be important determinants of benthic diatom assemblages in streams. *Freshwater Biology*, **26**, 279-294.

Stevenson R.J., Peterson C.G., Kirschtel D.B., King C.C. & Tuchman N.C. (1991) Density-dependent growth, ecological strategies and effects of nutrients and shading on benthic diatom succession in streams. *Journal of Phycology*, **27**, 59-69.

Tett P., Gallegos C., Kelly M.G., Hornberger G.M. & Cosby B.J. (1978) Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. *Limnology and Oceanography*, **23**, 785-797.

Tilman D. (1977) Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology*, **58**, 338-348.

Tilman D. (1989) Chapter #6. *Perspectives in Ecological Theory* (Eds. J. Roughgarden, R.M. May & S.A. Levin), p. 394. Perspectives in Ecological Theory, Princeton University Press.

Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, **8**, 36-50.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, **31**, 265-275.

Uehlinger U. (1991) Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv fur Hydrobiologie*, **123**, 219-237.

Vaughn C.C. (1986) The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). *Freshwater Biology*, **16**, 485-493.

Vogel S. (1981) *Life in Moving Fluids*. Princeton University Press. 352p.

Walton S.P., Welch E.B. & Horner R.R. (1995) Stream periphyton response to grazing and changes in phosphorus. *Hydrobiologia*, **302**, 31-46.

Welch E.B., Quinn J.M. & Hickey C.W. (1992) Periphyton biomass related to point-source nutrient enrichment in seven New Zealand streams. *Water Research*, **26**, 669-675.

Wetzel R.G. (1983) Attached algal-substrata interactions: fact or myth, and when and how ? *Periphyton of Freshwater Ecosystems* (Ed. R.G. Wetzel), pp. 207-216. Periphyton of Freshwater Ecosystems, Dr W. Junk Publishers.

Whitton B.A. (1975) Algae. *River Ecology* (Ed. B.A. Whitton), pp. 81-105. River Ecology, University of California Press.

Winterbourn M.J. & Fegley A. (1989) Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, South Island, streams. *New Zealand Natural Sciences*, **16**, 57-65.

# Chapter 7

## Periphyton development in three hydraulic reaches of a New Zealand foothills river: test of the disturbance - nutrient supply - grazer concept

**Preface**

In the previous chapter I developed a disturbance - resource supply - grazer conceptual model to explain, and predict, mean periphyton biomass and community structure in streams. In the following chapter, I describe a test of this model. This was achieved by monitoring periphyton biomass and community structure in headwater, mid-catchment and lowland reaches of a South Island foothills river and comparing the data with that predicted by the model based on the disturbance regimes and cellular nutrient concentrations at the sites.

## I. Introduction

Broad scale studies have isolated two fundamental factors controlling patterns in periphyton biomass and community structure among streams: flood disturbance frequency (reflecting catchment properties of climate, geology and physical morphology) and degree of nutrient supply (reflecting different aspects of climate and geology, as well as landuse). Biggs (1988) reported that disturbance-related parameters explained 62% of the variance in periphyton ash-free dry mass during summer in New Zealand streams and that nutrient supply parameters explained a further 15.6%. Fisher & Grimm (1988) reported that 67% of the temporal variance in periphyton biomass in a Sonoran Desert stream was explained by disturbance, but only an additional 4% by nutrients. In contrast to this, Biggs & Close (1989) reported that 69% of the mean monthly chlorophyll *a* over a year among nine streams was explained by nutrients and only 25% by disturbance. However, strong colinearity between disturbance and nutrient concentrations was also found. In Chapter 2 I reported that 86.5% of the variance in mean monthly chlorophyll *a* over a year at 16 other New Zealand streams was explained by disturbance and nutrient supply, and suggested that these parameters could be used as axes to develop a conceptual habitat template model for periphyton in unshaded streams. Such a model is developed in Chapter 6 and is summarised again in Fig. 7.1.

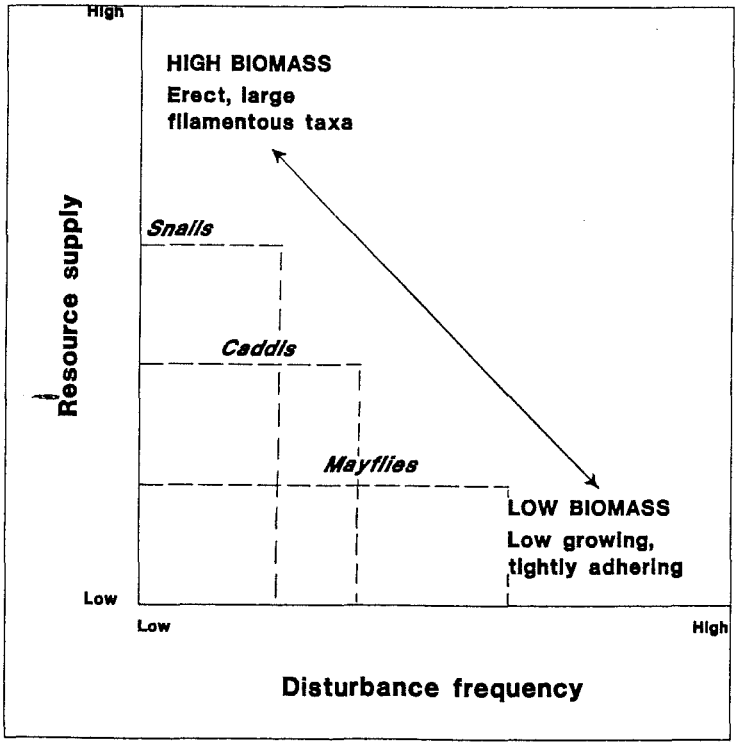


Fig. 7.1: Stream periphyton disturbance - nutrient supply conceptual model. The regions delineated under 'Snails', 'Caddis' and 'Mayflies' are where these groups of invertebrates are most likely to exert strong grazer effects on periphyton development in relation to direct disturbance and productivity of the periphyton community (see Chapter 6).

In the following study, I test the utility of the disturbance - resource supply - grazer conceptual model. While the concept was developed based on patterns of periphyton among many streams, I considered that a good test of it would be to see if periphyton development could be predicted as a function of changes in habitat within a catchment (e.g., Vannote et al. 1980, Statzner & Higler 1986).

Brussock et al. (1985) identified three distinct regions along a "typical" river: (1) a headwater region, with a narrow channel confined within a typically V-shaped valley, a steep valley gradient (although the channel profile may be stepped), turbulent flow, and substrata dominated by bedrock, boulders and cobbles; (2) a mid-catchment region characterised by a much broader valley with flood plain development, often including braiding, active channel migration and bank erosion, a moderate valley gradient (with well defined pool-riffle-run sequences), moderate velocities with turbulent flow being confined to occasional steep riffles, and substrata dominated by cobbles and gravels; and (3) a lowland region, with a very broad valley and associated floodplain within which the active river meanders as a single thread channel. The lowland valley gradient is low resulting in low water velocities and a substratum of gravels and sands that can be active at discharges less than bankful. The abundance of fine substrata and low relief dampens riffle formation and the bedforms that are created are easily modified by single flood events (Brussock et al. 1985).

Superimposed on this physical template can be gradients in light and nutrient regimes (Vannote et al. 1980). In headwater reaches with forested catchments, extensive riparian shading can occur (e.g., De Nicola et al. 1990). In many catchments however, there is a downstream reduction in forest cover and intensification of landuse. This can lead to greatly enhanced nutrient supply to lowland reaches (e.g., Holmes & Whitton 1981).

Several short-term, seasonal studies have been carried out in attempts to define responses of periphyton communities to downstream changes in habitat structure and to "test" predictions of the River Continuum Concept (Minshall et al. 1983, Bott et al. 1984, Naiman et al. 1987, Wiley et al. 1990). Communities have rarely been found to change in a manner which follows the idealised river continuum, however. Instead, most appear to respond more strongly to localised physical habitat and nutrient conditions (e.g., Wiley et al. 1990). In this study I hypothesised: (1) that average periphyton biomass would increase downstream where flood disturbance was expected to decrease and nutrient supply increase; and (2) that community structure would change from dominance by low profile taxa, competitive under conditions of low nutrient supply in upstream reaches, to communities dominated by architecturally more complex, nutrient demanding taxa in downstream reaches.

## II. Study area

The study was carried out in the Kakanui River of North Otago in the South Island (Fig. 7.2). The upper catchment is composed of steep hill-country at an altitude of > 500 m and the vegetation is largely dominated by native snow-tussock grass oversown with pastoral grasses and fertilised for extensive cattle and sheep grazing. Agriculture intensifies in mid-catchment where hills are much lower (< 500 m) and native tussock grasses have been largely converted to improved pasture supporting high stock densities. In the lower catchment (< 100 m altitude) the pastures are even more highly developed and supported intensive sheep and cattle grazing. Much of the upper basin is underlain by schistose rock. However, the lower catchment is an outwash plain underlain by Tertiary sediments.

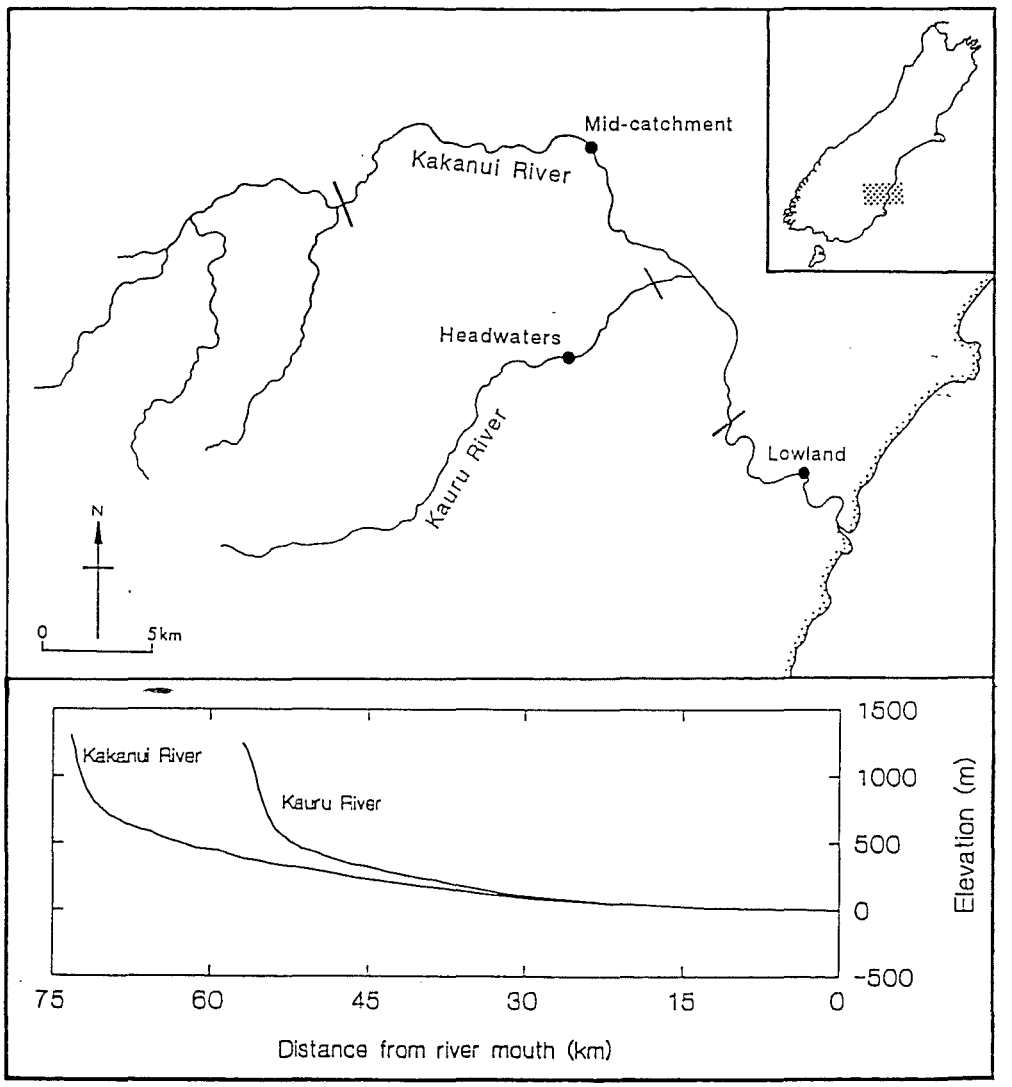


Fig. 7.2: Map of Kakanui River study area, location of the three study sites, and a longitudinal profile based on altitude. Lines across the Kakanui and Kauru Rivers delimit boundaries between 'headwater', 'mid-catchment' and 'lowland' reaches.

The river could be divided into three hydraulic reaches based on channel form following Brussock et al. (1985). The 'headwater reach' (Fig. 7.2, Table 7.1), encompassed a V-shaped valley with a stepped pool-riffle channel and was dominated by boulder and bedrock substrata. It extended from first order rivulets to 4th order streams. A progressive decrease in channel slope, and an associated increase in the proportion of runs, occurred at the head of the mid-catchment reach as the 5th order streams coalesced to form the 6th order river. Here the substratum was dominated by cobbles and gravels. Bedrock formed the channel banks of some sections. Approximately half way down this reach the river left the confines of the foothills and entered an outwash plain. Areas of Tertiary bedrock intersected the river at various points and created localised hydraulic controls. The bed was dominated by a cobble-gravel substratum, with braids in a number of locations. The gradient of the river fell further about 5 -7 km from the sea where the 'lowland reach' effectively began. Here the river was more confined with a single, narrow, channel dominanted by runs. Gravels dominated the substratum of runs and cobbles occurred in the occasional riffles. In this reach the river meandered for a short distance before entering the Kakanui Estuary. Several ox-bow formations were heavily colonised by aquatic macrophytes, and water cress and *Ranunculus* sp. also grew in patches along the river margin and in slower flowing parts of the main channel in this reach. Sites were selected as representative of these reaches and were close to flow monitoring stations. The headwater site received a small amount of shading from riparian willow trees and an adjacent pine-tree plantation during parts of the day in winter.

## III. Materials and methods

*Field procedures*

Flows were monitored at each site by the Otago Regional Council using pressure transducer water level recorders. Rating curves were developed based on monthly gaugings which covered a full range of flows. Periphyton samples were collected on each visit from September 1992 to June 1994. Sampling on some occasions (particularly in summer of 1993/94; Fig. 7.3) was missed due to high flows which made access to the river too dangerous. The width of the river was divided into 5 equal sections along a single transect for each riffle and another for each run, and the depth and velocity at the mid-point of each was measured with a Gurley current meter and wading rod. Riffles were defined as steep, rapidly flowing sections with broken surface water and runs were lower gradient sections with relatively uniform flows and an unbroken water surface. The stone beneath each of the mid points on the transects was lifted from the bed and transported to the bank where a known area was defined on the top surface, and the material from within it scraped off with a

scalpel. The five samples from each transect were pooled and returned, chilled, to the laboratory where they were frozen for later analysis.

Regression equations were developed between discharge and mean water velocity for runs and riffles at each sampling site. They enabled discharge to be converted to velocity for the sampling period, and velocity exceedance statistics were calculated as described in Chapter 2. Coefficients of determination were generally between 0.72 and 0.78 for all equations except for the riffle at the mid-catchment site where there was no significant relationship.

At the time of each periphyton sampling, a water sample was collected in a sterile 120 ml specimen container and frozen until analysis for soluble nutrients (Smith et al. 1982). Temperature and conductivity were measured in the field. Substrate particle size was assessed at each site on one occasion using the Wolman method (Mosley 1983). One hundred particles were randomly selected, from a run and from a riffle.

*Laboratory procedures*

Upon thawing, periphyton samples were blended and sub-sampled for analysis of chlorophyll *a* (extracted in boiling 90% ethanol). Ash-free dry mass (AFDM) (dried at 105°C for 24 h and ashed at 400°C for 4 h) was determined on a further subsample. Sub-samples were also analysed for N and P as total Kjeldahl N and total P normalised to AFDM to give mat nutrient concentrations ($\%N_C$, $\%P_C$) as described by Biggs & Close (1989). Analyses include all nutrients sorbed to inorganic particles, organic detritus, and bacteria/fungi.

Periphyton community structure was determined seasonally using an inverted microscope. Aliquots of each sample were scanned at 480x and 780x magnification to estimate the dominant taxon based on their contribution to the sample's biovolume (i.e., a visual integration of frequency x size). All other taxa were then rated on an 8 point scale in relation to the dominant taxon. If two taxa were co-dominant they were both given a score of 8. Generally one or, at most, three taxa made up approximately 70% of the community.

*Data analysis*

The average number of floods per year was determined as the number of events when velocities rose over 1 m $s^{-1}$ (see Chapter 2). Velocity intensity ($V_{80}$) was determined as the 80th percentile velocity from a cumulative frequency distribution of velocities for the 2 year study period. This incorporated flood peaks and their recessions, and is interpreted to be a measure of the intensity of velocity stress at the sites.

Geometric means and percent coefficients of variation were calculated for most variables because the data were non-normally distributed. One-way and two-way analyses of variance were used to test for differences among site and habitat treatments.

Shifts in periphyton community structure caused by a flood disturbance at the upland site and community recovery following this flood were analysed using principal components analysis. This involved calculating "factor" scores which represent a statistical combination of common taxa which are highly correlated in their abundance. Factor-1 represents a group of the most common taxa which are all highly correlated in their relative abundance over time and factor-2 represents the second most highly correlated group of taxa, but which are oriented orthogonally in principal components space to the first group of taxa (i.e., factor-1). The factor scores for each sampling occasion were then used as co-ordinates to graph shifts in the relative balance of factor-1 and factor-2 species over time in principal components space. These points were then joined according to the consecutive sampling sequence to demonstrate changes in community structure with disturbance and recovery.

To test the disturbance - nutrient supply model (Chapter 6) the locations of the sites/habitats were plotted according to disturbance frequency and cellular nitrogen co-ordinates. This enabled the ranges for stream-bed chlorophyll *a* to be predicted and compared with actual values. A quantitative test for predicting mean monthly chlorophyll *a* was then carried out by inserting disturbance frequency and cellular nitrogen concentrations in the following regression equation (see Chapter 2):

$\text{Log}_e$ mean monthly chlorophyll *a* (mg $m^{-2}$) = 1.053 - 0.067 (floods $yr^{-1}$) + 0.764 (% cellular N) $R^2 = 0.865$

Predicted values of chlorophyll *a* for each riffle and run at the three sites were then plotted against observed values to indicate goodness of fit.

For community structure, the seasonal relative abundance scores were averaged for individual taxa and habitats. These taxa scores were then manually transcribed to a disturbance frequency/nutrient supply matrix consisting of nine cells (representing different community guilds) defined by different combinations of disturbance and cellular N, and with guild position of the taxa being determined as in Chapter 6. After taxa scores had been entered on the matrix they were summed for each of the nine cells. Habitat template bubble plots were then constructed whereby the diameter of the bubbles in each cell represented the summed abundance scores for that cell. This was to identify the predominant guild found in

each habitat. These plots were then evaluated against a plot of where on the matrix the site/habitat was located based on its disturbance - % $N_c$ statistics to test the accuracy/robustness of the disturbance - resource guild concept of Chapter 6.

## IV. Results

*Hydrology and hydraulics*

*Average conditions*

Mean and median flows increased down the catchment as tributaries coalesced and channel gradient decreased (Table 7.1). Hydraulic conditions at the times of sampling displayed expected differences between riffles and runs, with depths being greater and velocities lower in the runs (Table 7.2). The degree of variability in velocity and Froude number was much less in riffles than runs over the sampling period.

Among-reach differences occurred for depth, velocity and Froude number in the runs, but not necessarily as predicted from downstream changes in channel gradient (Table 7.2). For example, velocities in the run at the lowland site were the highest recorded.

Hydraulic conditions of riffles among the reaches were more similar than for runs with depths averaging 15 - 20 cm and velocities 58 - 69 cm $s^{-1}$. The velocities of riffles in the three reaches were not significantly different (Table 7.2). The Froude numbers of these habitats were quite high (over twice those of the run habitats) indicating moderately high shear stresses.

Table 7.1 Summary of selected physico-chemical characteristics of the study sites (1, determined from full flow record). ANOVA *F* values: ** P<0.01, *** P<0.001, n.s. not significant.

| | Site/Catchment Location | | | ANOVA |
|---|---|---|---|---|
| | Headwater | Mid-catchment | Lowland | *F* |
| **Physical** | | | | |
| Distance from sea (km) | 36 | 33 | 5.5 | - |
| Slope of reach (%) | 1.24 | 0.38 | 0.15 | - |
| Mean flow[1] ($m^3$ $s^{-1}$) | 1.32 | 3.19 | 5.40 | - |
| C.V. flow (%) | 2.86 | 2.31 | 3.04 | - |
| Median flow[1] ($m^3$ $s^{-1}$) | 0.57 | 1.68 | 2.55 | - |
| **Chemical** | | | | |
| Temperature (°C) | 10.58 | 10.43 | 10.63 | n.s. |
| $Conductivity_{25}$ (mS $m^{-1}$) | 6.2 | 6.5 | 9.4 | *** |
| $NO_3$-N (mg $m^{-3}$) | 35 | 22 | 116 | ** |
| DRP (mg $m^{-3}$) | 6 | 5 | 7 | n.s. |
| $NO_3$:DRP | 5.14 | 3.49 | 17.74 | *** |

Bed sediments were predominantly coarse cobbles, boulders and bedrock in the headwater reach, coarse cobbles and boulders in the mid-catchment reach, and smaller cobbles in the lowland reach (Table 7.2). Thus, changes in sediment size were more or less as expected along a channel of decreasing gradient. In the headwater reach, bedrock made up 18% of the riffle substratum area and 47% of that in the run. The remaining areas comprised a mixture of loosely packed boulders, cobbles and some gravel. Field observations of substrata at the mid- and lower-catchment sites indicated they were very stable with much interlocking of particles.

*Flood flows*

There were two periods of frequent, high intensity, flooding at the beginning and end of the study period (June - November 1992 and November 1993 - March 1994). Between these was one period of moderate instability (November - February 1993) followed by a further two prolonged periods of high stability (February - May 1993 and May - September 1993). These periods of stability were separated by single flood events (Figs 7.3, 7.4, 7.5).

Table 7.2 Summary of hydraulic and periphyton characteristics measured at the sampling sites. ANOVA *F* values: * $P<0.05$, ** $P<0.01$, *** $P<0.001$. Statistics with same superscript for a given parameter are not significantly different from each other at $P<0.05$ as evaluated using a post-hoc Tukey test. The periphyton statistics were calculated as geometric means.

| | | Runs | | | | Riffles | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Sites | | | ANOVA | Sites | | | ANOVA |
| | | Head | Mid | Low | *F* | Head | Mid | Low | *F* |
| **Hydraulics** | | | | | | | | | |
| Depth (m) | *x* | $0.26^{1}$ | $0.50^{1,2}$ | $0.48^{2}$ | *** | $0.15^{1}$ | $0.20^{1,2}$ | $0.21^{2}$ | * |
| | (%CV) | (40.5) | (22.7) | (17.6) | | (33.1) | (37.0) | (35.2) | |
| Velocity (m $s^{-1}$) | *x* | $0.30^{1}$ | $0.19^{1}$ | $0.33^{2}$ | * | 0.69 | 0.58 | 0.64 | n.s. |
| | (%CV) | (59.5) | (49.9) | (57.4) | | (31.0) | (27.0) | (37.4) | |
| Froude No. | $\tilde{x}$ | $0.20^{1}$ | $0.08^{2}$ | $0.15^{1}$ | *** | $0.59^{1}$ | $0.45^{2}$ | $0.46^{2}$ | ** |
| | (%CV) | (50.8) | (41.7) | (50.5) | | (22.8) | (26.8) | (24.4) | |
| Flood events >1 m $s^{-1}$ (no. $y^{-1}$) | *x* | 6 | 1.5 | 7 | | 11 | 7.5 | 10.5 | - |
| $V_{80}$(m $s^{-1}$) | *x* | 0.44 | 0.25 | 0.64 | | 0.85 | - | 1.04 | - |
| $D_{50}$(mm) | *x* | 256 | 83 | 46 | | 147 | 100 | 35 | |
| **Periphyton** | | | | | | | | | |
| Chlorophyll *a* (mg $m^{-2}$) | *x* | 10.1 | 17.0 | 8.6 | n.s. | $18.0^{1}$ | $13.7^{1}$ | $59^{2}$ | ** |
| | (%CV) | (88.7) | (48.3) | (83.0) | | (76.6) | (31.8) | (16.6) | |
| AFDM (g $m^{-2}$) | *x* | 6.2 | 15.1 | 5.6 | n.s. | 10.7 | 14.5 | 21.6 | n.s. |
| | (%CV) | (84.9) | (50.5) | (56.8) | | (84.9) | (27.6) | (17.9) | |
| % Chlorophyll *a* | *x* | 0.20 | 0.13 | 0.21 | n.s. | $0.21^{1}$ | $0.12^{2}$ | $0.30^{1}$ | *** |
| | (%CV) | (60.5) | (59.7) | (58.9) | | (58.9) | (84.0) | (42.2) | |
| $\%P_c$ | *x* | 0.29 | 0.40 | 0.35 | n.s. | 0.28 | 0.27 | 0.37 | n.s. |
| | (%CV) | (35.6) | (45.8) | (43.7) | | (72.8) | (40.4) | (33.6) | |
| $\%N_c$ | *x* | 3.37 | 3.81 | 4.22 | n.s. | $3.02^{1}$ | $3.34^{1}$ | $4.94^{2}$ | * |
| | (%CV) | (28.7) | (14.6) | (21.3) | | (85.8) | (23.7) | (11.9) | |
| $N_c$:$P_c$ | *x* | 11.8 | 9.7 | 12.0 | n.s. | 10.8 | 12.5 | 13.3 | n.s. |
| | (%CV) | (15.6) | (18.1) | (10.9) | | (38.4) | (20.8) | (6.8) | |

The annual frequency of flood events where water velocities exceeded 1 m $s^{-1}$ was highest in riffles at 7.5 - 11 per year (Table 7.2), and lowest in the runs, particularly at the mid-catchment site (1.5 per year). The 80% velocity exceedances indicate that the flow regime at the lowland riffle site was the most extreme (Figs 7.3, 7.4, 7.5). Little bed movement and channel re-shaping was observed at any site except during a major flood in December 1993 when bar formations were altered, most severely at the lowland site.

*Periphyton*

Average biomass

Chlorophyll *a* and AFDM concentrations were low in the runs at all sites, and did not vary significantly among them (Table 7.2). Concentrations were similarly low in the riffles, except at the lowland site where they were significantly higher than the other riffles. Chlorophyll *a* concentration was higher in riffles than runs at the headwater and lowland site, but the reverse was the case at the mid-catchment site. Variability in both parameters decreased in riffles down the catchment, but such a decrease was not evident in runs. The percentage of periphyton biomass as chlorophyll *a* varied significantly among sites with the mid catchment site having a low value and the lowland site having a relatively high value. This difference can be seen by comparing AFDM with chlorophyll *a* concentrations in Figs 7.4 and 7.5.

Chlorophyll *a* concentration and AFDM differed significantly between riffles and runs, but there were no significant differences for the habitats among the reaches (Table 7.3). The interaction term of site and habitat was also significant for chlorophyll *a* suggesting that the degree of difference between riffle and run varied among the sites. Conversely, percentage chlorophyll *a* did not differ significantly between runs and riffles, but did differ among the reaches.

Community structure

Periphyton community structure was similar in runs of the three reaches in spring and summer, even though biomass was greatly different among them (Table 7.4). The diatoms *Gomphoneis herculeana*, *Synedra ulna* and *Cymbella kappii* were dominant or abundant. However, the three reaches had distinctly different communities in autumn and winter when biomass was highest. The headwater reach was dominated by the filamentous cyanobacteria *Lyngbya* sp. and *Tolypothrix* sp. The mid-catchment reach was dominated by the diatom *Epithemia sorex* and the colonial blue-green alga *Nostoc* sp. The lowland reach was dominated by *Nostoc* sp. and *Synedra ulna*. Thus, community structure in the runs was similar in spring and summer, but differed in autumn and winter when there was a shift toward a predominance of the nitrogen fixing taxa *Nostoc* and *Epithemia* at the

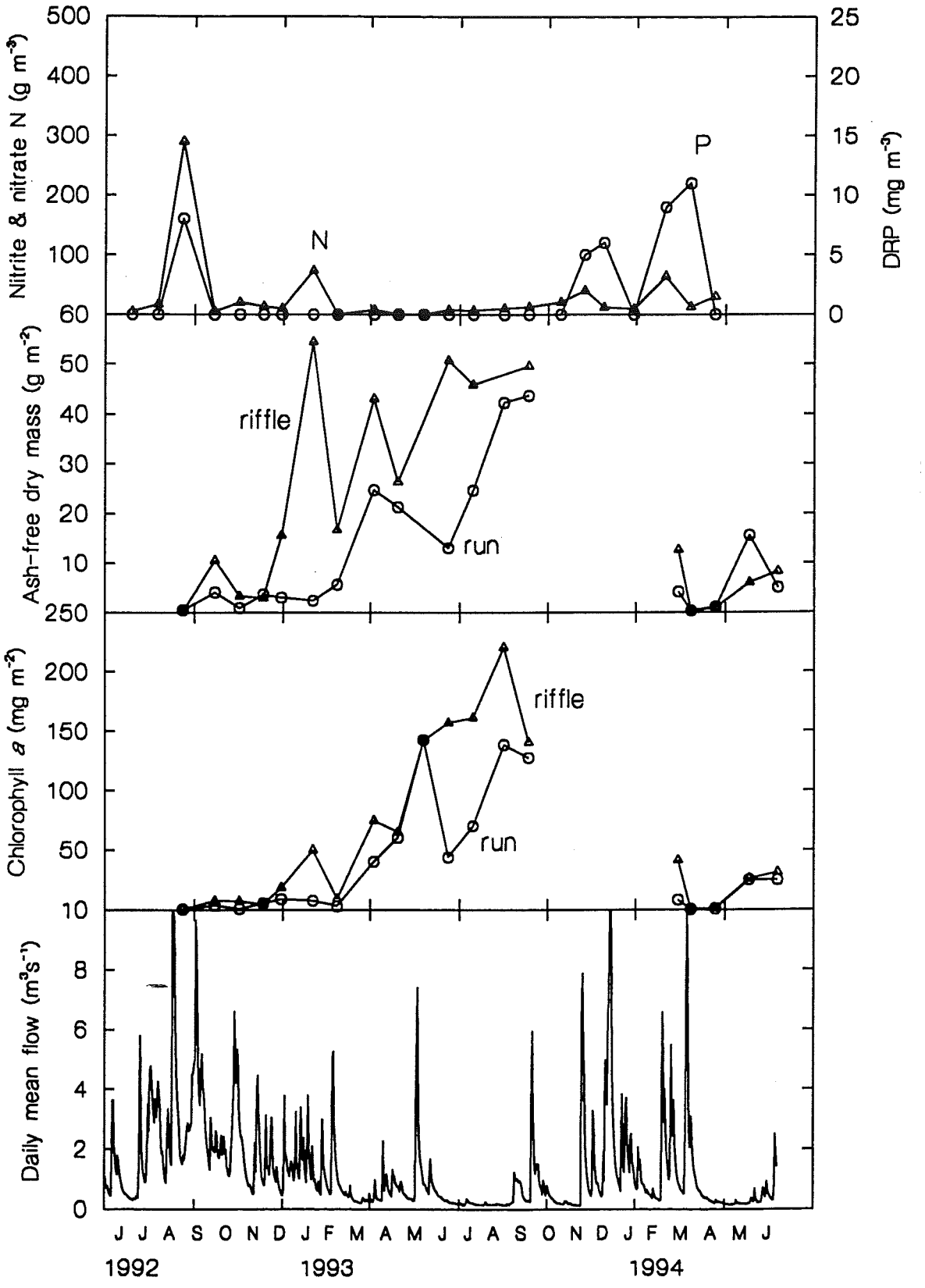


Fig. 7.3: Temporal fluctuations in water nutrients, periphyton ash-free dry mass, chlorophyll *a* concentration and flow at the headwater site (Kauru River).

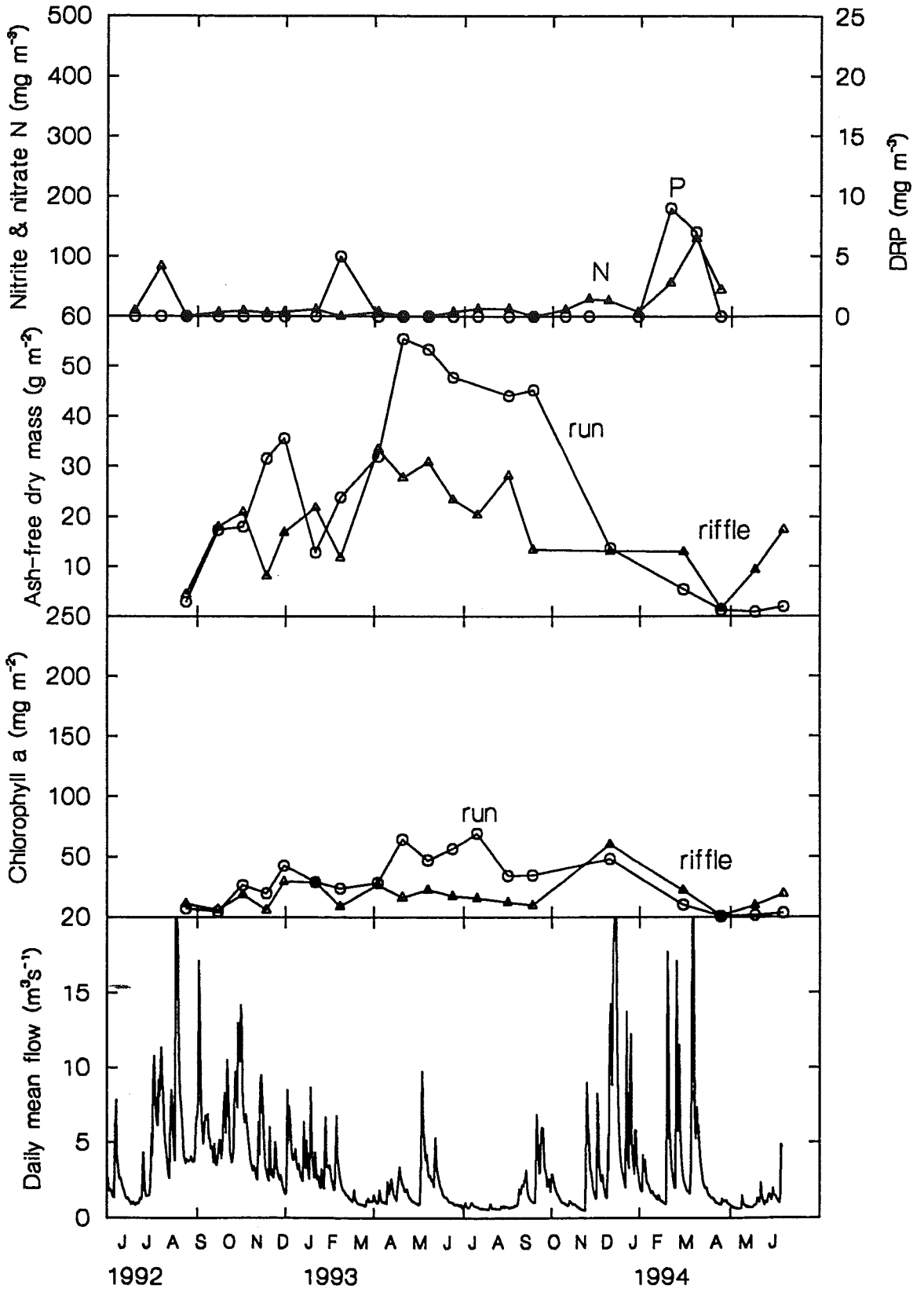


Fig. 7.4: Temporal fluctuations in water nutrients, periphyton ash-free dry mass, chlorophyll *a* concentration and flow at the mid-catchment site (Clifton Falls, Kakanui River).

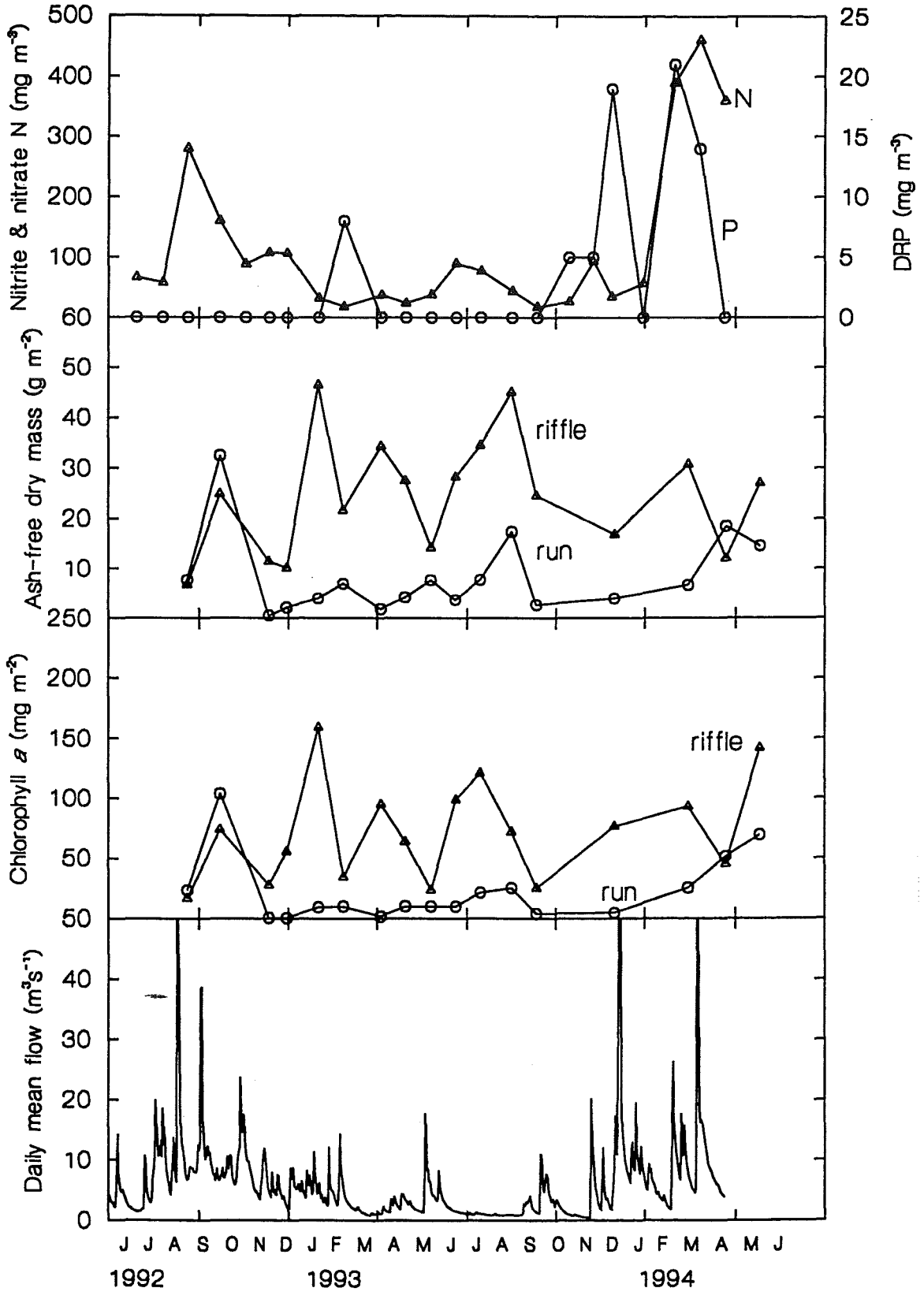


Fig. 7.5: Temporal fluctuations in water nutrients, periphyton ash-free dry mass, chlorophyll *a* concentration and flow at the lowland site (Pringles, Kakanui River).

Table 7.3 ANOVA of three periphyton parameters as a function of location in the catchment (Site) and hydraulic habitat (Habitat). Chlorophyll *a* and AFDM were log transformed for this analysis.

| | Source | Sum of squares | DF | *F* | *P* |
|---|---|---|---|---|---|
| 1. | **Chlorophyll *a*** | | | | |
| | Site | 5.08 | 2 | 0.982 | 0.378 |
| | Habitat | 15.94 | 1 | 6.165 | 0.015 |
| | Site × Habitat | 20.72 | 2 | 4.007 | 0.021 |
| | Error | 268.84 | 104 | | |
| 2. | **AFDM** | | | | |
| | Site | 6.88 | 2 | 2.205 | 0.115 |
| | Habitat | 10.57 | 1 | 6.774 | 0.011 |
| | Site × Habitat | 8.68 | 2 | 2.779 | 0.067 |
| | Error | 162.30 | 104 | | |
| 3. | **% Chlorophyll *a*** | | | | |
| | Site | 0.31 | 2 | 12.16 | 0.000 |
| | Habitat | 0.02 | 1 | 1.59 | 0.211 |
| | Site × Habitat | 0.06 | 2 | 2.28 | 0.108 |
| | Error | 1.322 | 104 | | |

mid-catchment and lowland reaches. These later taxa generally formed a thicker, more architecturally complex, community than the tightly adhering, low growing, filamentous *Lyngbya* and *Tolypothrix* communities that dominated the headwater reach.

Communities in the riffle of the headwater reach were markedly different in spring/summer and autumn/winter. During the warmer months, diatoms (*Diatoma hiemale, Gomphoneis herculeana* and *Synedra ulna*) dominated the reach. However, in the cooler autumn and winter period the headwater reach was dominated by filamentous cyanobacteria (*Lyngbya* and *Tolypothrix*) and diatoms were still abundant. These autumn-winter communities had the highest biomass of any sampled.

Table 7.4 Relative abundance, and associated biomass of periphyton taxa in runs at the Kakanui River study sites in four seasons.

| | Headwater | | | | Mid-catchment | | | | Lowland | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sp. | Sum. | Aut. | Win | Sp. | Sum. | Aut. | Win | Sp. | Sum. | Aut. | Win. |
| 1) Taxa | | | | | | | | | | | | |
| Chlorophyta | | | | | | | | | | | | |
| *Ankistrodesmus* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Gloeocystis* sp. | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Mougeotia* sp. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Oedogonium* sp. | 0 | 3 | 5 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 0 |
| *Spirogyra* sp. | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 |
| *Stigeoclonium* sp. | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ulothrix zonata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Bacillariophyta | | | | | | | | | | | | |
| *Achnanthes* sp. | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 4 | 0 | 1 | 0 |
| *Achnanthidium lanceolatum* | 3 | 3 | 3 | 1 | 4 | 2 | 2 | 1 | 5 | 3 | 0 | 4 |
| *Achnanthidium minutissimum* | 3 | 3 | 4 | 2 | 3 | 2 | 2 | 2 | 5 | 3 | 3 | 3 |
| *Cocconeis* sp. | 1 | 2 | 2 | 3 | 1 | 0 | 1 | 1 | 0 | 4 | 2 | 0 |
| *Cymbella kappii* | 3 | 3 | 4 | 4 | 7 | 4 | 1 | 3 | 7 | 2 | 4 | 4 |
| *Cymbella minuta* | 1 | 3 | 2 | 4 | 4 | 3 | 1 | 2 | 4 | 3 | 3 | 4 |
| *Diatoma* sp. | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Diatoma hiemale* | 7 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Epithemia sorex* | 0 | 2 | 1 | 1 | 0 | 6 | 8 | 8 | 0 | 0 | 1 | 1 |
| *Fragilaria vaucheriae* | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Gomphoneis herculeana* | 8 | 8 | 5 | 5 | 7 | 5 | 2 | 3 | 7 | 8 | 4 | 3 |
| *Gomphonema* sp. | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 3 | 4 | 3 | 3 |
| *Gomphonema acuminatum* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Gomphonema constrictum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| *Melosira varians* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Navicula avenacea* | 0 | 2 | 6 | 5 | 1 | 5 | 7 | 6 | 0 | 0 | 1 | 1 |
| *Navicula cryptocephala* | 1 | 1 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 1 |
| *Rhopalodia novae zelandiae* | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 4 | 0 | 0 | 0 | 0 |
| *Surirella* sp. | 0 | 3 | 1 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Synedra rumpens* | 4 | 3 | 3 | 1 | 3 | 3 | 1 | 3 | 3 | 6 | 3 | 5 |
| *Synedra ulna* | 6 | 2 | 7 | 7 | 8 | 8 | 1 | 5 | 8 | 5 | 3 | 8 |
| *Tabellaria flocculosa* | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 |
| Unidentified | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 2 |
| Rhodophyta | | | | | | | | | | | | |
| *Auduoinella hermanii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Cyanobacteria | | | | | | | | | | | | |
| *Lyngbya* sp. | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 4 | 0 |
| *Nostoc* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 8 | 0 |
| *Phormidium* sp. | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 |
| *Tolypothrix* sp. | 0 | 6 | 0 | 8 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| 2) Biomass | | | | | | | | | | | | |
| Chlorophyll *a* (mg $m^{-2}$) | 3.7 | 7.4 | 143 | 138 | 4.6 | 43 | 64 | 69 | 104 | 0.1 | 9.7 | 21 |
| Ash-free dry mass (g $m^{-2}$) | 4.1 | 2.4 | 75 | 42 | 17 | 36 | 56 | 65 | 33 | 2.2 | 6.9 | 7.7 |

Conversely, riffles in both the mid-catchment and lowland reaches were dominated by filamentous green algae *(Mougeotia, Oedogonium* sp. and *Spirogyra)* in summer, autumn and winter, with the diatoms *Gomphoneis herculeana* and *Synedra ulna* being co-dominant or abundant. In spring, the riffles of these reaches were dominated by the later two diatoms plus *Cymbella kappii* (Table 7.5). Thus, the riffle at the headwater reach was most commonly dominated by diatoms which were capable of tight adhesion (Chapter 5) and tightly adhering filamentous cyanobacteria, whereas the mid-catchment and lowland sites were more commonly dominated by the architecturally more complex filamentous green algae.

Temporal dynamics

Temporal sequences in periphyton biomass at the headwater and mid-catchment sites appeared to be controlled more by variations in discharge than by season. As noted earlier, frequent floods occurred from July to December 1992 and again from November to March, 1994 (Figs 7.3, 7.4, 7.5). Between these periods, three distinct periods of stable flow occurred. During the periods with frequent floods, periphyton biomass in both runs and riffles was much lower at all sites (Table 7.6). The difference was most pronounced, and highly significant in runs and riffles, at the headwater site. Over all sites, AFDM in the riffles was most affected by high flows. Variability in both chlorophyll *a* concentrations and AFDM was lower during periods of low variability in flows.

Following high flows, cycles of accrual and sloughing occurred at the headwater site, but these became less pronounced downstream (Figs 7.3, 7.4, 7.5). An accrual sequence in the headwater run from March to June 1994 is replotted at a larger scale in Fig. 7.6. Prior to the flood on 19 March, chlorophyll *a* concentration was low and communities consisted predominantly of diatoms (mostly *Gomphoneis herculeana* and *Gomphonema* cf. *angustatum*). Sampling done 4 days after the flood (at the headwater site only), showed that most of the biomass had been removed. The little periphyton that was collected then contained a variety of diatoms, none of which was clearly more abundant than any other. They included *Gomphoneis herculeana, Synedra ulna, Tabellaria flocculosa, Cymbella* sp., *Navicula* sp., *Achnanthidium* sp. A 40 - 50 day period of re-colonisation followed, with peak biomass and carrying capacity being reached after approximately 70 days. No succession of species occurred in the community. Instead *Gomphoneis herculeana* resumed its dominance over the entire accrual cycle, with the other pre-flood taxa also being important. Only *Synedra ulna* and *Cymbella minuta* increased in relative abundance after the flood.

Table 7.5 Relative abundance, and associated biomass of periphyton taxa in riffles at the Kakanui River study sites, in four seasons.

| | Headwater | | | | Mid-catchment | | | | Lowland | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sp. | Sum. | Aut. | Win. | Sp. | Sum. | Aut. | Win. | Sp. | Sum. | Aut. | Win. |
| 1) Taxa | | | | | | | | | | | | |
| Chlorophyta | | | | | | | | | | | | |
| *Ankistrodesmus* sp. | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| *Gloeocystis* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Mougeotia* sp. | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 8 | 0 | 0 | 3 | 0 |
| *Oedogonium* sp. | 0 | 2 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 8 | 7 |
| *Spirogyra* sp. | 0 | 1 | 0 | 0 | 0 | 8 | 8 | 0 | 0 | 8 | 7 | 0 |
| *Stigeoclonium* sp. | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 |
| *Ulothrix zonata* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 3 |
| Bacillariophyta | | | | | | | | | | | | |
| *Achnanthes* sp. | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 3 | 0 | 2 | 0 |
| *Achnanthidium lanceolatum* | 3 | 1 | 3 | 4 | 4 | 2 | 2 | 3 | 4 | 2 | 2 | 6 |
| *Achnanthidium minutissima* | 2 | 1 | 4 | 3 | 4 | 2 | 3 | 3 | 3 | 2 | 3 | 4 |
| *Cocconeis* sp. | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 3 |
| *Cymbella kappii* | 2 | 2 | 3 | 4 | 5 | 3 | 1 | 5 | 8 | 1 | 4 | 3 |
| *Cymbella minuta* | 3 | 1 | 2 | 4 | 3 | 4 | 1 | 1 | 5 | 1 | 4 | 4 |
| *Diatoma* sp. | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Diatoma hiemale* | 8 | 0 | 2 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Epithemia sorex* | 0 | 0 | 4 | 5 | 1 | 4 | 5 | 5 | 1 | 0 | 0 | 0 |
| *Fragilaria vaucheriae* | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| *Gomphoneis herculeana* | 8 | 8 | 5 | 5 | 8 | 5 | 8 | 7 | 8 | 0 | 3 | 0 |
| *Gomphonema* sp. | 2 | 0 | 3 | 0 | 0 | 0 | 3 | 2 | 2 | 1 | 4 | 3 |
| *Melosira varians* | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Navicula avenacea* | 0 | 0 | 6 | 2 | 0 | 3 | 3 | 4 | 0 | 0 | 1 | 0 |
| *Navicula cryptocephala* | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 2 |
| *Rhopalodia novae zelandiae* | 0 | 0 | 0 | 0 | 3 | 3 | 3 | 3 | 0 | 0 | 0 | 0 |
| *Surirella* sp. | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 2 | 0 | 0 | 0 | 0 |
| *Synedra rumpens* | 4 | 0 | 4 | 7 | 3 | 3 | 1 | 3 | 3 | 3 | 2 | 3 |
| *Synedra ulna* | 7 | 1 | 7 | 6 | 7 | 3 | 3 | 8 | 8 | 2 | 7 | 8 |
| *Tabellaria flocculosa* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| Unidentified | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 5 | 1 | 0 | 0 | 3 |
| Rhodophyta | | | | | | | | | | | | |
| *Auduoinella hermanii* | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 1 | 1 | 3 |
| Cyanobacteria | | | | | | | | | | | | |
| *Lyngbya* sp. | 0 | 0 | 8 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 3 | 0 |
| *Phormidium* sp. | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| *Tolypothrix* sp. | 0 | 3 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| 2) Biomass | | | | | | | | | | | | |
| Chlorophyll *a* (mg $m^{-2}$) | 7.4 | 50 | 142 | 220 | 5.9 | 29 | 16 | 15 | 73 | 55 | 64 | 121 |
| Ash-free dry mass (g $m^{-2}$) | 11 | 55 | 61 | 67 | 18 | 17 | 28 | 20 | 25 | 10 | 28 | 35 |

Table 7.6 Comparison of chlorophyll *a* concentration and AFDM concentrations for runs and riffles during high flow variability periods and low flow variability periods. T-test values: *** P <0.001.

| Site / Habitat | | | Runs | Riffles |
|---|---|---|---|---|
| **Chlorophyll *a*** | | | | |
| Headwater | - high variability | $x$ | 1.6 | 2.8 |
| | | (%CV) | (2.96) | (204) |
| | - low variability | $x$ | 38.1 | 70.0 |
| | | (%CV) | (34) | (23) |
| | | T-test *P* | *** | *** |
| Mid-catchment | - high variability | $x$ | 10.7 | 11.5 |
| | | (%CV) | (63) | (50) |
| | - low variability | $x$ | 23.7 | 15.6 |
| | | (%CV) | (39) | (15) |
| | | T-test *P* | n.s. | n.s. |
| Lowland | - high variability | $x$ | 3.2 | 47.7 |
| | | (%CV) | (286) | (16) |
| | - low variability | $x$ | 11.8 | 68 |
| | | (%CV) | (43) | (17) |
| | | T-test *P* | n.s. | n.s. |
| **AFDM** | | | | |
| Headwater | - high variability | $x$ | 1.6 | 2.49 |
| | | (%CV) | (212) | (182) |
| | - low variability | $x$ | 16.5 | 30.9 |
| | | (%CV) | (37) | (24) |
| | | T-test *P* | *** | *** |
| Mid-catchment | - high variability | $x$ | 9.9 | 9.4 |
| | | (%CV) | (52) | (39) |
| | - low variability | $x$ | 20.6 | 20.0 |
| | | (%CV) | (48) | (14) |
| | | T-test *P* | n.s. | * |
| Lowland | - high variability | $x$ | 4.22 | 14.3 |
| | | (%CV) | (120) | (20) |
| | - low variability | $x$ | 6.1 | 28.8 |
| | | (%CV) | (39) | (11) |
| | | T-test P | n.s. | ** |

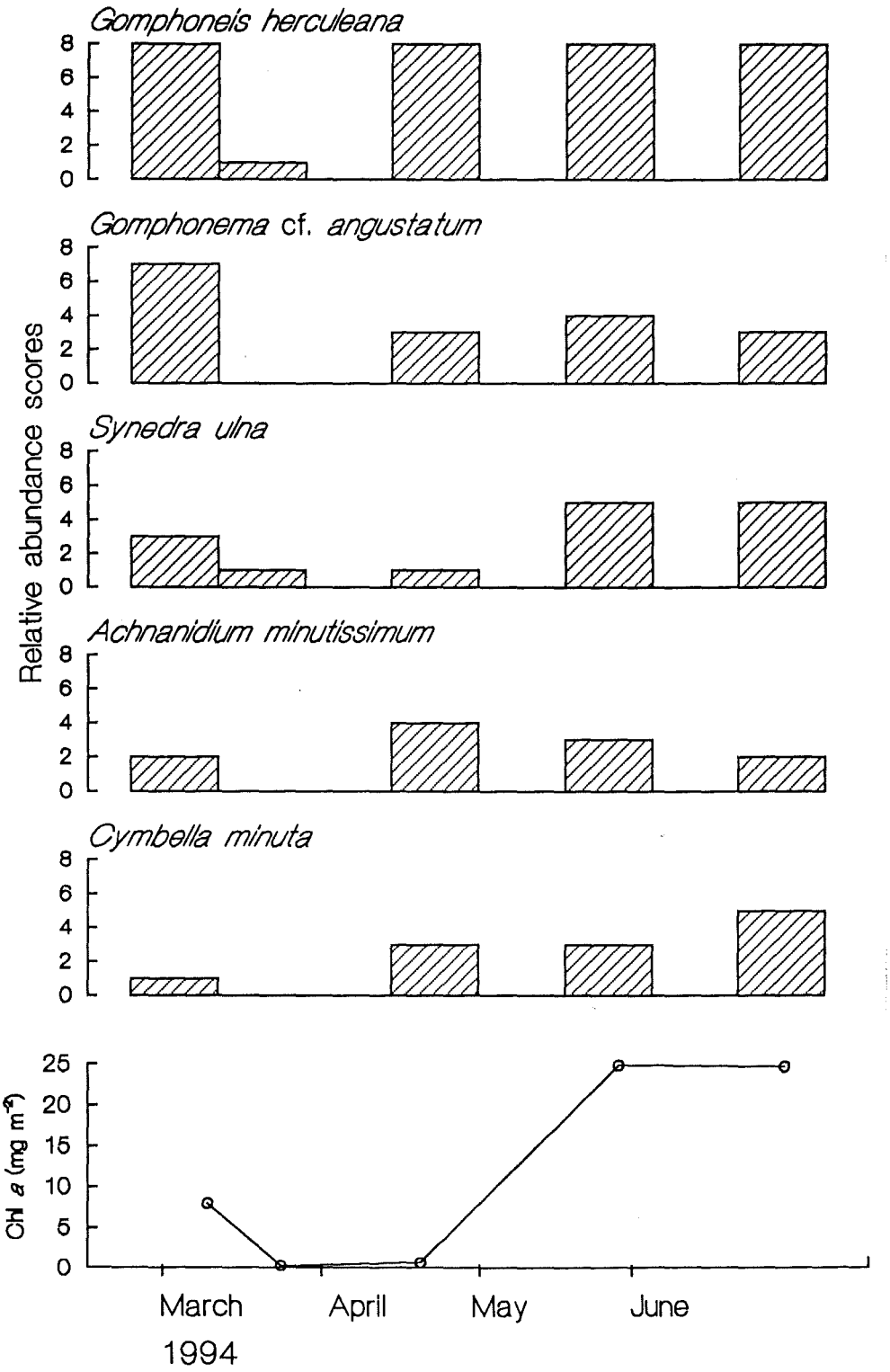


Fig. 7.6: Chlorophyll *a* accrual, and dominant taxa, in a run at the headwater site following a major flood on 19 March 1994. The first column is the sampling 10 days prior to the flood. The relative abundance of the taxa are shown on a scale of 0 (absent) to 8 (dominant).

Conversely, pre-flood biomass was much higher in the riffle, and the flood had a more devastating effect in terms of biomass lost (Fig. 7.7). As with the run, the community was dominated by the diatom *Gomphoneis herculeana.* However, two filamentous green algae were also abundant *(Oedogonium* sp. and *Spirogyra* sp.). These taxa were completely eliminated from this habitat by the high flows and did not return within the time of the study. The sampling immediately after the flood showed a variety of diatoms similar to that found in the run (*Gomphoneis herculeana, Cymbella* sp., *Synedra ulna, Achnanthidium* sp.; plus *Epithemia sorex* and *Rhoicosphenia curvata*). As in the run there was a prolonged period of regeneration, but a lower rate of growth. *Gomphoneis herculeana* also resumed its dominance by the time colonisation was complete.

An analysis of temporal shifts in the first two principal components of the communities over the flood - regeneration period gives a measure of relative structural dynamics of the periphyton as a function of disturbance (Fig. 7.8). Prior to the flood the run and riffle communities had quite different locations in principal components space reflecting their distinctly different structures [the high relative abundance of diatoms in the runs (represented by Factor-1) and the high relative abundance of filamentous taxa (Factor - 2) in the riffles]. Immediately following the flood both run and riffle communities had similar compositions. By the second post-flood sampling (approx. 30 days following the flood), communities in both habitats had regenerated to a state similar to the pre-flood run community (but with a much lower biomass, Figs 7.6, 7.7). However, following this the run community continued to develop strongly along factor-1, whereas the riffle community started to separate in principal component space and develop more along Factor-2 (toward the pre-flood condition). These results suggested that succession away from dominance by a common group of initial colonists, and back to a mature community reflecting the physical conditions of each habitat, was taking > 30 days at this site.

Table 7.7 lists the relative abundance of common taxa in runs at all three sites 10 days before and 30 days after the same flood. The flood caused a change in dominant taxa at the mid-catchment and lowland sites. As noted previously, *Gomphoneis herculeana* was somewhat resistant to the flood at the headwater site and it remained the dominant taxon after the flood. Other moderately resistant taxa included *Cymbella kappii* and the branched red alga *Audouinella hermanii.* Taxa that generally decreased in relative abundance after the flood included *Stigeoclonium* sp., *Epithemia sorex* and *Synedra rumpens.*

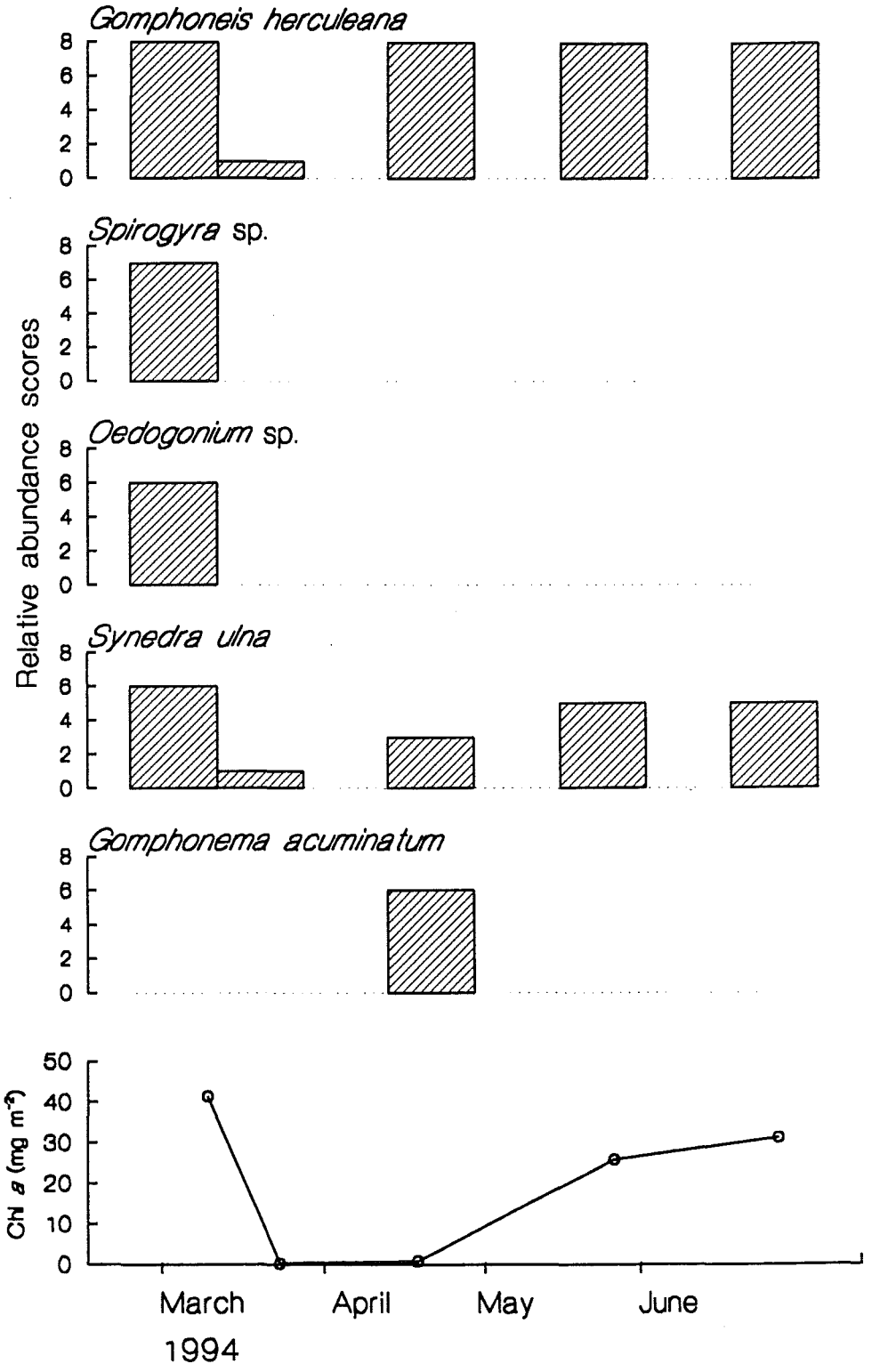


Fig. 7.7: Chlorophyll *a* accrual, and dominant taxa, in a riffle at the headwater site following a major flood on 19 March 1994. The first column is the sampling 10 days prior to the flood.

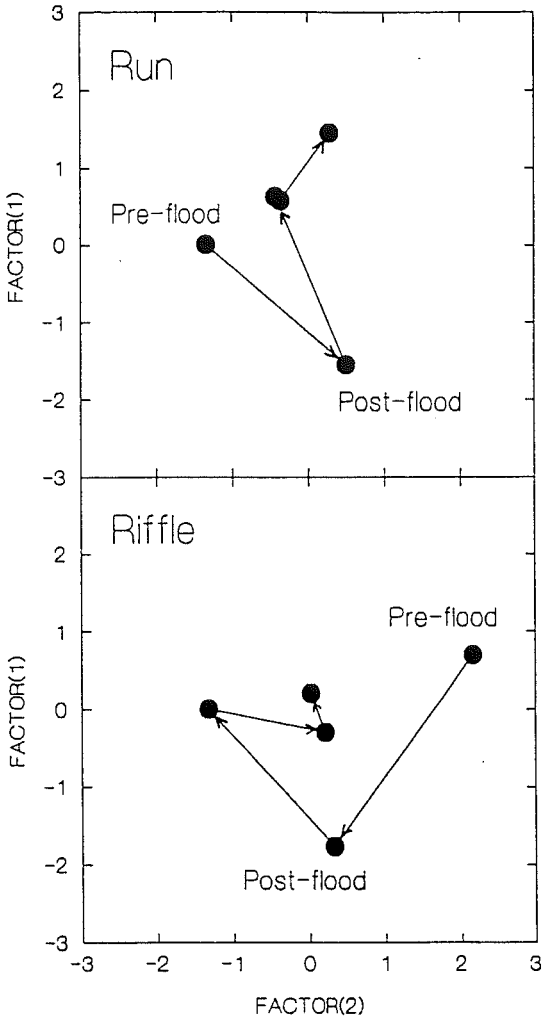


Fig. 7.8: Shifts in principal component factor scores for run and riffle communities as a result of flood disturbance in the headwater site (Kauru River). Principal components were calculated on the pooled run and riffle data. Pre-flood sampling was on 9 March '94, the flood occurred on 19 March, and post-flood sampling was on 19 April, 25 May and 20 June.

*Downstream gradient in enrichment*

Nutrient concentrations in the water were generally low at all sites (Table 7.1), but with higher concentrations of nitrogen at the lowland site. There was generally little temporal variation in water nutrients. The highest concentrations recorded at all three sites were during the prolonged periods of high flow at the beginning and near the end of the study (Figs 7.3, 7.4, 7.5). Ratios of nitrate nitrogen to dissolved reactive phosphorus were always <72 (the highest recorded at the lowland site in April 1994) and were usually considerably lower. N:P ratios for the mid-catchment and headwater sites were, with one exception, < 4 during the first 14 months of periphyton sampling.

Cellular nutrient concentrations (Table 7.2) were low, but with a trend for cellular N to increase moving downstream. Percentage N values were significantly different ($P$ <0.05) in the riffles among the hydraulic reaches indicating that the lowland reach was more enriched. There was only one significant difference in cellular nutrients between runs and riffles at the

sites. This occurred for $\%P_C$ at the mid-catchment site. The ratio of cellular nutrients ($N_C$:$P_C$) was between 9.7 and 13.3 for the different habitats and reaches which indicated that the communities were probably nitrogen limited.

Table 7.7 Summary of relative abundance of common periphyton taxa in runs before (9 March) and after (19 April) the flood on 19 March, 1994.

| Taxa | Headwater | | Mid-catchment | | Lowland | |
|---|---|---|---|---|---|---|
| | Before | After | Before | After | Before | After |
| Chlorophyta | | | | | | |
| *Oedogonium* sp. | 0 | 3 | 0 | 3 | 5 | 5 |
| *Stigeoclonium* sp. | 0 | 0 | 1 | 0 | 6 | 0 |
| *Ulothrix zonata* | 3 | 0 | 0 | 0 | 0 | 5 |
| Bacillariophyta | | | | | | |
| *Achnanthidium lanceolatum* | 1 | 1 | 2 | 3 | 3 | 3 |
| *Achnanthidium minutissimum* | 2 | 4 | 2 | 3 | 3 | 1 |
| *Cocconeis* sp. | 1 | 3 | 0 | 1 | 1 | 1 |
| *Cymbella kappii* | 3 | 3 | 2 | 6 | 6 | 6 |
| *Cymbella minuta* | 1 | 3 | 3 | 4 | 8 | 4 |
| *Epithemia sorex* | 3 | 0 | 8 | 6 | 0 | 0 |
| *Gomphonema* cf. *angustatum* | 7 | 3 | 3 | 5 | 1 | 2 |
| *Gomphonema acuminatum* | 0 | 4 | 0 | 0 | 0 | 0 |
| *Gomphoneis herculeana* | 8 | 8 | 3 | 5 | 2 | 0 |
| *Melosira varians* | 0 | 1 | 0 | 1 | 3 | 5 |
| *Navicula avenacea* | 0 | 0 | 0 | 0 | 1 | 5 |
| *Navicula cryptocephala* | 1 | 0 | 1 | 3 | 3 | 1 |
| *Synedra rumpens* | 2 | 1 | 3 | 2 | 8 | 4 |
| *Synedra ulna* | 3 | 1 | 1 | 8 | 4 | 7 |
| Rhodophyta | | | | | | |
| *Auduoinella hermanii* | 0 | 2 | 2 | 0 | 5 | 8 |

*Testing predictions of the 'Disturbance - Resource Supply - Grazer' model*

Fig. 7.9 summarises a disturbance - resource supply periphyton habitat matrix and the linear 'best-fit' contours for chlorophyll *a* concentration based on data in Chapter 2. The locations of the Kakanui River sites/habitats are also shown as functions of their mean annual frequency of disturbances and cellular nitrogen concentrations. This plot identifies that the three riffle sites had a medium frequency of disturbance events relative to the rivers studied elsewhere in New Zealand, while the runs had a medium to low frequency (the run at the mid-catchment site had a low frequency). Nutrient concentrations at all sites were moderate, except for the lowland riffle where nutrient levels were moderate to high. A comparison of

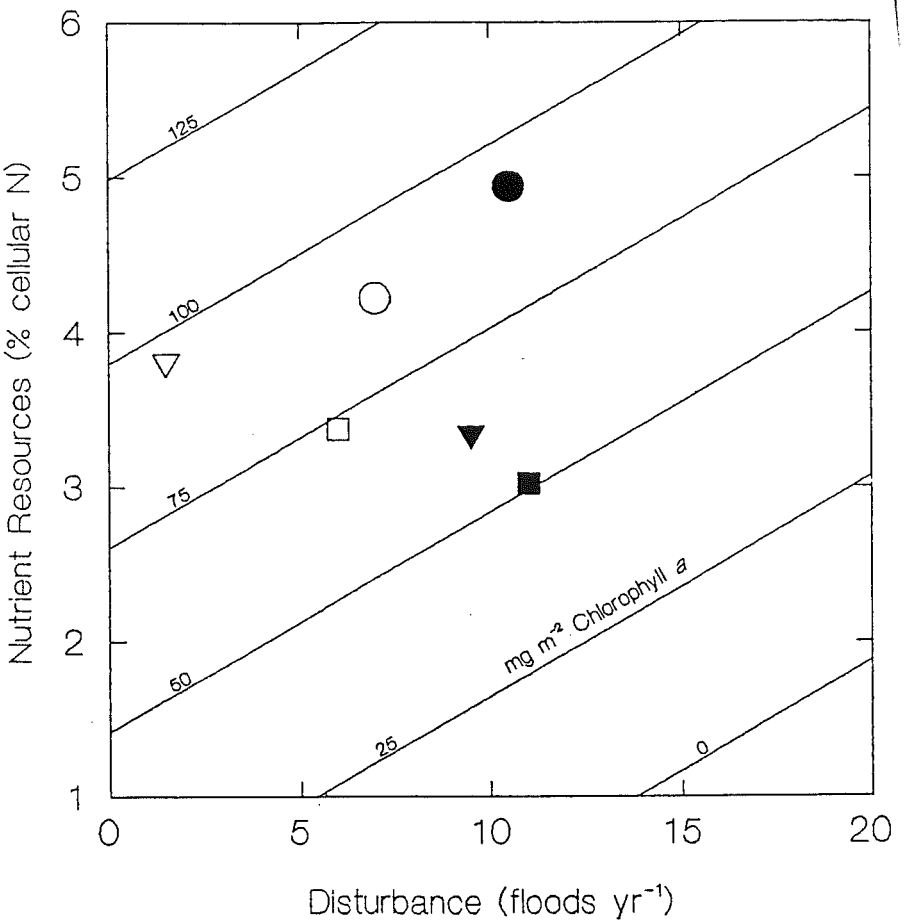


Fig. 7.9: Location of the sites/habitats on the disturbance - nutrient supply conceptual model (see Chapter 6). Chlorophyll *a* concentration contours calculated from data in Chapter 2 are also shown. Squares represent the headwater reach, triangles the mid-catchment reach and circles the lowland reach. Open symbols indicate runs and closed symbols riffles.

the location of the sites as functions of disturbance and cellular nutrient concentrations with the chlorophyll *a* contours suggests average chlorophyll *a* should range from 50 mg $m^{-2}$ for the upper catchment riffle to around 80 mg $m^{-2}$ for the mid-catchment run and lowland riffle. It also suggests that habitats at the upper and lower catchment sites, and the mid-catchment riffle should be dominated by moderately nutrient competitive and moderately disturbance resistance taxa. In contrast, the mid-catchment run communities should be dominated by moderately nutrient competitive taxa which are typically found in low disturbance habitats.

Quantitative predictions of chlorophyll *a* concentrations showed good agreement with values observed in riffles over a wide range of values (Fig. 7.10). However, the agreement for run communities was poor. Chlorophyll *a* concentration was 60% lower in the headwater run than was expected from the model, 65% lower in the mid-catchment run,

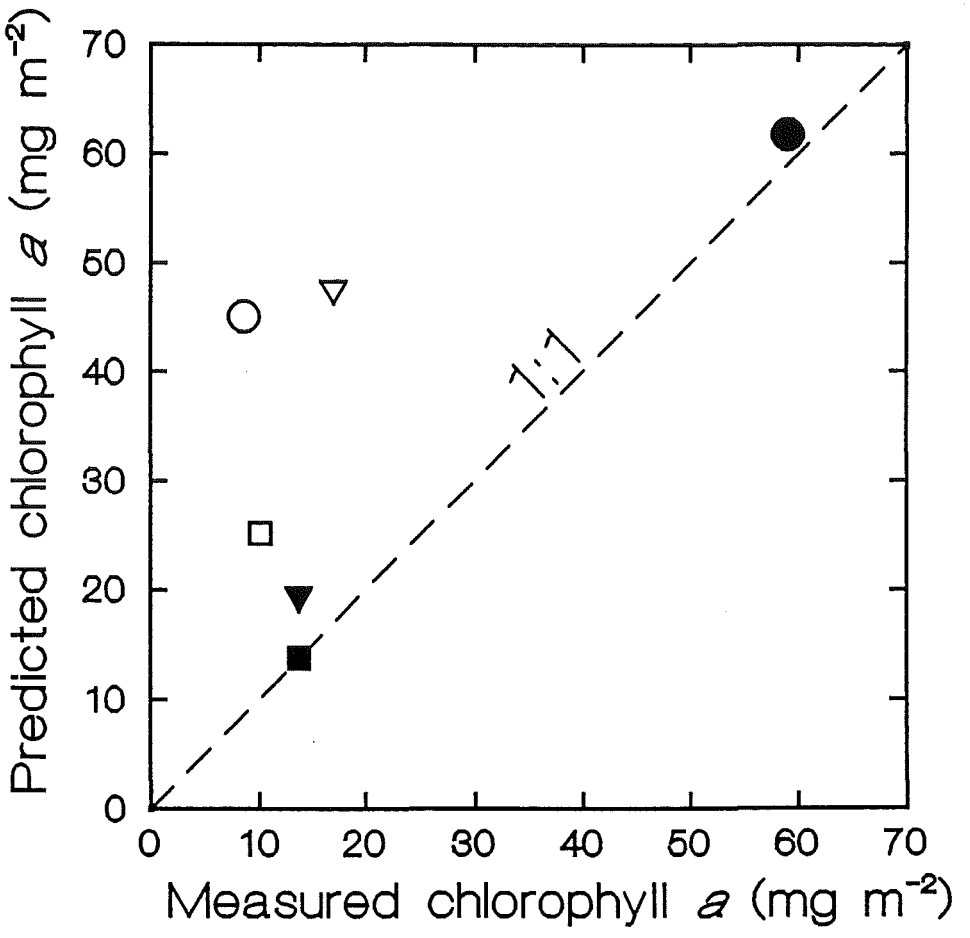


Fig. 7.10: Observed mean monthly chlorophyll *a* vs. that predicted from the disturbance - nutrient supply model. Squares represent the headwater reach, triangles the mid-catchment reach and circles the lowland reach. Open symbols indicate runs and closed are riffles.

and 80% lower in the lowland run. These deviations may be attributable to the impact of snail grazing in these locations (see Discussion).

Algal taxa were allocated to one of nine combinations of disturbance resistance and nutrient demand based on the classification given in Fig. 6.3 of Chapter 6. The relative abundance scores for each cell were then summed and "bubble" plots drawn with the relative diameter of the bubbles being proportional to the sum of the abundance scores (Fig. 7.11). The location and relative size of the bubbles in Fig. 7.11 indicates that all sites were dominated by taxa which I classified as moderately nutrient demanding and moderately disturbance-resistant (see Chapter 6). Comparing the location of the largest bubble for each site with the location of the site on the disturbance - nutrient resource matrix (based on measure values for disturbance frequency and nutrient supply; Fig. 7.9) indicates that

community structure largely conforms to that predicted from disturbance - nutrient supply variables and provides support for the classifications in Chapter 6.

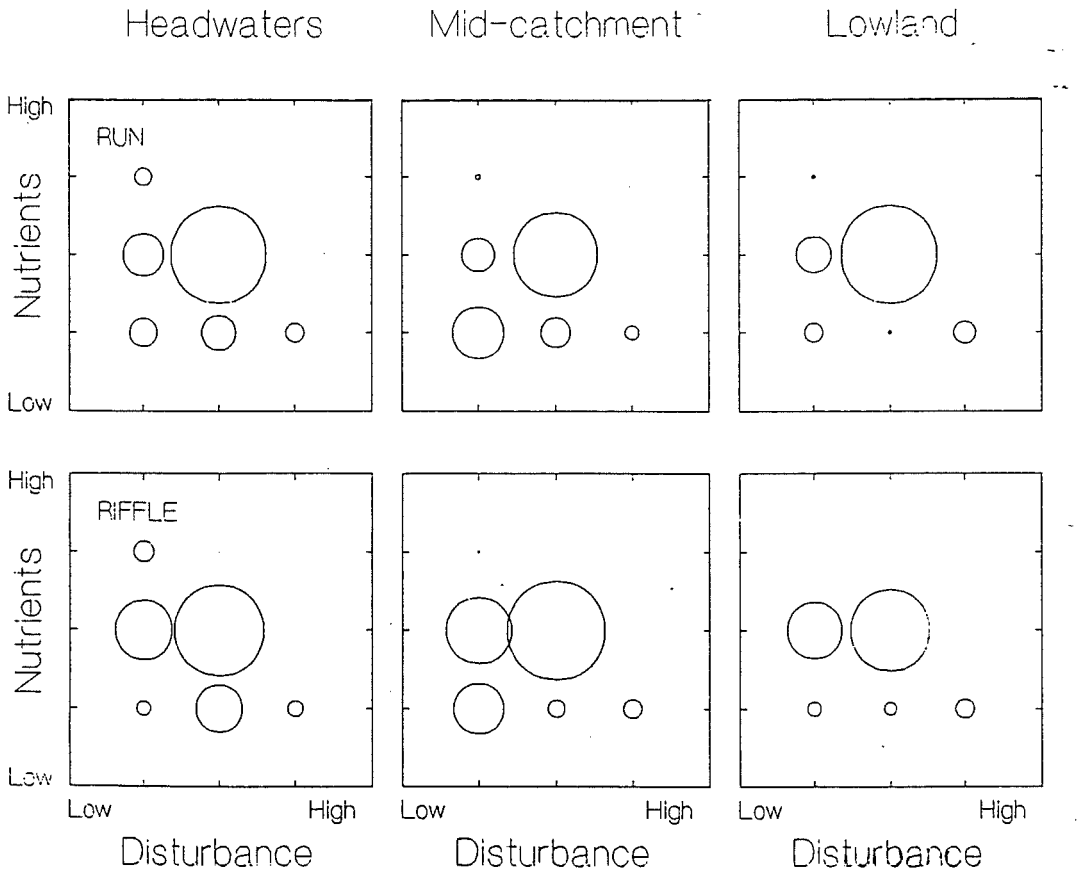


Fig. 7.11: Bubble plots for the sites in the disturbance - nutrient supply guilds/sub-guilds (see Fig. 6.3). The diameter of each bubble is proportional to the sum of the abundance scores of taxa present at the given site that have been classified as belonging to that cell of the habitat matrix (Fig. 6.3).

The more enriched lowland site had fewer taxa characteristic of low nutrient environments, and the mid-catchment site (riffle and run) and headwater riffle also had relatively higher abundances of low disturbance-resistant taxa.

## V. Discussion

I expected that mean water depth should increase, velocity and Froude number should decrease, and levels of enrichment should increase from headwaters to lowland reaches in the study river. However, I found that although enrichment increased, changes in mean site hydraulics of both runs and riffles did not conform to this idealised model. While runs and

riffles in the headwater reach were significantly shallower, and riffle Froude numbers were higher, there were no general trends between the mid-catchment and lowland reaches. Indeed, mean run velocities were highest in the lowland reach. Broad scale changes in catchment slope, and the aggregation of tributary inflows, only resulted in partial changes in hydraulic conditions at the scale of the individual sampling transect. Conversely, a more general downstream increase in the level of enrichment was found. This was also demonstrated by levels of cellular nitrogen, the largest increase in $\%N_C$ being between the mid-catchment and lowland reaches (mean $\%N_C$ of riffle communities increased by 48% between these reaches) where agricultural development of the catchment was most intensive. Habitat constraints for periphyton growth were therefore more complex than initially predicted from the simple channel form-catchment enrichment model. However, algal communities did develop in a predictable way as a function of both local disturbance and nutrient supply constraints.

My disturbance - nutrient model (Chapter 6), predicted that the average biomass of periphyton should be higher in the more enriched, lower disturbance habitats of the lowland reach, and that the communities there should be dominated by high profile, nutrient-demanding, taxa. I also predicted the converse of this for the more disturbance-prone, unenriched, headwater habitats. There was good agreement with the disturbance - resource supply component of the model predictions in all respects except for chlorophyll *a* concentrations in runs (see below).

Periphyton communities in runs within all three reaches were dominated by a similar group of diatoms in spring and summer. However, in autumn and winter headwater communities were dominated by filamentous cyanobacteria/diatoms, whereas communities in the mid-catchment and lowland reaches were dominated by both nitrogen fixing cyanobacteria and diatoms. In the riffles, however, there was a clear separation between headwater communities and the other reaches. While the headwater reach was dominated by diatoms (spring/summer) and cyanobacteria (autumn/winter), the mid-catchment and lowland reaches were dominated by filamentous green algae and diatoms (summer/autumn/winter). These changes in riffle communities among reaches most closely reflected the magnitude of differences in depth and Froude number among the reaches. However, for the runs hydraulic conditions did not change systematically down the catchment, and even though there was progressive enrichment downstream, community differences were generally not as large as for riffles (and with few trends). Thus, my initial hypotheses were largely rejected for the runs, but accepted for the riffles.

In an earlier study, Biggs & Lowe (1994) surveyed periphyton biomass and physical/nutrient characteristics of eight run sites on the Kakanui River during summer low flows (February 1992). We found that the snail *Potamopyrgus antipodarum* had densities of 2,000 - 10,000 $m^{-2}$ on unglazed tile substrata and they were able to track areas of high periphyton production on nutrient diffusing substrates where densities increased to > 20,000 $m^{-2}$. Grazing by these animals prevented significant increases in periphyton biomass in runs of the lowland section of the river. It is therefore possible that the deviation of chlorophyll *a* in the runs from that predicted quantitatively using the 'disturbance - nutrient supply' multiple regression equation (see Methods) was due to these grazing effects. In Chapter 6, I recognise that such snail grazing activity could be an important loss mechanism for biomass and modify the predictions of the model in habitats where disturbance frequency was moderate - low (Fig. 7.1).

Such strong grazing activity may not only affect mean periphyton biomass in runs, but also alter community structure and seasonal dynamics. It is likely that the absence of filamentous green algae from runs, and their predominance in riffles of the more enriched mid-catchment and lowland sites during summer/autumn/winter (and also the more uniform dominance of diatoms in reaches in spring/summer) is a direct result of grazing by snails. During field work I noticed that snails disappeared into the interstices of the sediments in winter and it is likely that this, together with the more stable flow conditions, accounted for the winter peak in chlorophyll *a* and the differences in periphyton community structure between the sites.

I also found no difference in periphyton biomass in either the riffles or the runs between times of high and low flow variability at the mid-catchment and lowland sites, whereas a significant difference occurred at the headwater site. At the headwater site, almost half the bed material in the run and almost one fifth in the riffle was bedrock. However, the remaining bed particles were unconsolidated. This, combined with the greater slope of the reach, suggests that considerable bed movement is likely during high flows and is likely to be destructive of both the periphyton (Biggs & Close 1989) and invertebrates (Scrimgeour & Winterbourn 1989). When flows stabilise again, periphyton recolonisation and accrual is likely to be much faster for periphyton than invertebrates (Power 1992) resulting in significant biomass development which is largely unconstrained by grazing. At the mid-catchment and lowland sites bed materials were moderately coarse, but well consolidated, and the slopes of the reaches were low. Consequently, only the most severe floods (e.g., December 1994) would have re-worked the bed. Thus, snails and other less mobile grazers at these lower sites will be much less affected by smaller floods, and are likely to maintain grazing pressure on periphyton whether flows are variable or not. It appears that periphyton

communities in both runs and riffles at the headwater site are abiotically controlled for much of the year through flood disturbance and nutrient limitation during the interflood periods. However, this appears to switch in the runs of the more stable mid-catchment and lowland reaches to biotic control for much of the year.

## VI. Summary

In this study I monitored periphyton biomass, nutrient content and community structure in headwater, mid-catchment and lowland runs and riffles of a foothills river to determine how these communities varied spatially and temporally as a function of downstream changes in disturbance, hydraulics and nutrient supply. Site-specific predictions of community biomass and structure were then tested under the proposed disturbance - resource supply - grazer concept (Chapter 6). Mean monthly chlorophyll *a* concentration did not vary significantly ($P > 0.05$) among runs, but it did among riffles. Overall, the differences in periphyton biomass between runs and riffles were more significant than differences among hydraulic reaches. Periphyton community structure in the runs was similar among reaches in spring and summer, but in autumn and winter communities in the headwater reach were dominated by filamentous cyanobacteria whereas in the mid-catchment and lowland reaches they were dominated by nitrogen-fixing cyanobacteria and diatoms. Major differences in community structure occurred in riffles among the reaches. Riffle communities in the headwater reach were dominated by filamentous cyanobacteria and diatoms, whereas in the mid-catchment and lowland reaches filamentous green algae and diatoms were dominant. A downstream gradient in enrichment appeared to control biomass and community composition of riffle communities. However, run communities in the mid-catchment and lowland reaches showed no response to this enrichment gradient. Strong grazer activity during spring and summer appeared to override any response to hydraulics or nutrients in runs, and maintained biomass at low levels. The disturbance - resource supply - grazer concept predicted biomass and composition of periphyton communities well.

## VII. References

Biggs, B. J. F. (1988): Algal proliferations in New Zealand's shallow stony foothills rivers: towards a predictive model. - Verh. Int. Verein. Limnol. **23**: 1405-1411.

Biggs, B. J. F. & Close, M. E. (1989): Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. - Freshwat. Biol. **22**: 209-231.

Biggs, B. J. F. & Lowe, R. L. (1994): Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. - NZ Jnl. Mar. Freshwat. Res. **28**: 119-134.

Bott, T. L.; Brock, J. T.; Dunn, C. S.; Naiman, R. J.; Ovink, R. W. & Petersen, R. C. (1985): Benthic community metabolism in four temperate stream systems: An inter-volume comparison and evaluation of the river continuum concept. - Hydrobiologia **123**: 3-45.

Brussock, P. P.; Brown, A. V. & Dixon, J. C. (1985): Channel form and stream ecosystem models. - Wat. Resources Bull. **21**: 859-866.

De Nicola, D. M.; McIntire, C. D.; Lamberti, G. A.; Gregory, S. V. & Ashkenas, L. R. (1990): Temporal patterns of grazer-periphyton interactions in laboratory streams. - Freshwat. Biol. **23**: 475-489.

Fisher, S. G. & Grimm, N. B. (1988): Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. - Verh. Int. Verein. Limnol. **23**: 1183-1190.

Holmes, N. T. H. & Whitton, B. A. (1981): Phytobenthos of the River Tees and its tributaries. - Freshwat. Biol. **11**: 139-168.

Minshall, G. W.; Petersen, R. C.; Cummins, K. W.; Bott, T. L.; Sedell, J. R.; Cushing, C. E. & Vannote, R. L. (1983): Interbiome comparison of stream ecosystem dynamics. - Ecol. Monog. **53**: 1-25.

Mosley, M. P. (1983): Response of braided rivers to changing discharge. - J. Hydro. (NZ) **22**: 18-67.

Naiman, R. J.; Melillo, J. M.; Lock, M. A.; Ford, T. E. & Reice, S. R. (1987): Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. - Ecology **68**: 1139-1156.

Power, M. E. (1992): Hydrological and trophic controls of seasonal algal blooms in northern Californian rivers. - Arch. Hydrobiol. **125**: 375-410.

Scrimgeour, G. J. & Winterbourn, M. J. (1989): Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. - Hydrobiologia **171**: 33-44.

Smith, D. G.; Macaskill, J. B.; Stevenson, C. D. & Edgerley, W. H. L. (1982): Physical and chemical methods for water quality analysis. - Water and Soil Miscellaneous Publication No. 38. MWD, Wellington.

Statzner, B. & Higler, B. (1986): Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. - Freshwat. Biol. **16**: 127-139.

Vannote, R. L.; Minshall, G. W.; Cummins, K. W.; Sedell, J. R. & Cushing, C. E. (1980): The river continuum concept. - Can. J. Fish. Aquat. Sci. **37**: 130-137.

Wiley, M. J.; Osborne, L. L. & Larimore, R. W. (1990): Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. - Can. J. Fish. Aquat. Sci. **47**: 373-384.

# Chapter 8

## Disturbance of stream periphyton by hydrological scour under contrasting resource regimes: experimental test of the disturbance - resource supply - grazer concept

**Preface**

In Chapter 2, I demonstrated how patterns in periphyton biomass among unshaded streams can be controlled jointly by flood disturbance frequency and nutrient resources. Growth was supressed by the combined effects of low nutrient supply and high disturbance frequency, but with maximal growth occurring where nutrient supply was high and disturbance frequency was low. In Chapter 3, I experimentally investigated the disturbance resistance of periphyton commonly inhabiting low, compared with those in high, nutrient streams. Then in Chapter 4, I investigated resilience processes as affected by spatial variations in water velocity within streams. In Chapter 6, I integrated the results of these preceeding chapters with others from the literature and developed a conceptual model to explain how disturbance interacts with limiting resource supply and invertebrate grazing to control periphyton development in streams. This concept was then tested with data collected from a foothills river in Chapter 7. In the following chapter I investigate in more detail how resource supply affects the processes of disturbance resistance and resilience. I then use these results to carry out a further test of the disturbance - resource supply - grazer concept (Chapter 6). This study was experimental and was carried out at the University of Michigan Biological Station, Stream Research Facility, USA, using eight large (3.5m x 0.25m) outdoor experimental troughs. Both light and nutrient resources were manipulated. Light treatments were applied to half the lengths of all troughs using neutral density filters and four of the troughs had nutrients added continuously from a reservoir to saturate growth rates. A uniform (simulated) scouring disturbance was applied to all troughs during the exponential growth phase. A set of substrate tiles was removed from each resource treatment just prior to the disturbance and replaced immediately following it to act as a control against which the effects of the disturbance could be measured. Resistance was determined as the percentage biomass loss over the period of the disturbance, and resilience as rates of regrowth and time to return to pre-disturbance biomass.

## I. Introduction

The processes associated with joint flood disturbance - resource control of periphyton are likely to be highly complex, and strong interactions between the two variables may affect both resistance and resilience of communities. Where floods are infrequent and resource supply is high, inter-disturbance species recruitment and density dependent competition should lead to high profile, structurally complex, communities (e.g., dominated by filamentous green algae) and relatively high biomass (e.g., Lowe et al. 1986). In such habitats, resistance to scour disturbances should be low because skin friction and form drag will be high (e.g., Power and Stewart 1987, Peterson and Stevenson 1992, Chapter 3) (Fig. 8.1). Additionally, where nutrient resource supply is high, periphyton resilience should be high because specific growth rates increase as a direct function of nutrient availability (e.g., Bothwell 1989, DeAngelis et al. 1990). Low rates of resource supply may result in resource stressed layers at the base of the periphyton mat through density dependent resource depletion (Stevenson et al. 1991). Under such conditions, mats should not be strongly attached to the substratum and thus should also have moderately low resistance to flood disturbance (Biggs and Close 1989, Steinman et al. 1990, Peterson and Stevenson 1992) (Fig. 8.1). Further, because of the dependency of specific growth rates on resource supply, resilience in environments with low resource availability should also be low (DeAngelis et al. 1990), and should result in a low average and peak biomass in such habitats. Thus, under frequent flood disturbances

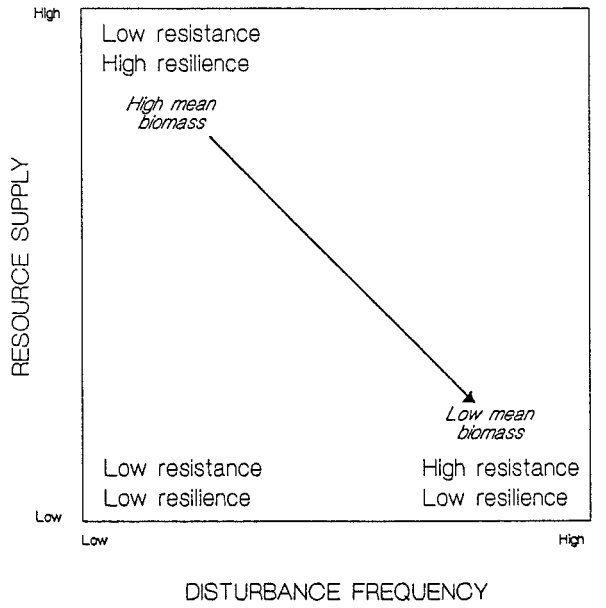


Fig. 8.1: Hypothesised shifts in resistance and resilience attributes in stream periphyton, and trends in biomass, as a function of inter-habitat gradients in disturbance frequency and resource supply over a year.

and high resource supply, high resistance and resilience should both be important attributes of the periphyton community (Fig. 8.1). Frequent disturbances select for highly resistant taxa such as low profile, prostrate, diatoms (e.g., Luttenton and Rada 1986, Robinson and Rushforth 1987, Peterson and Stevenson 1992), but under conditions of high resource supply the resilience of the remnant parts of the communities should be high and result in moderate average biomass. Peak biomass on the accrual cycle may never be attained if the return interval for disturbance is less than the time required for completion of accrual. However, if resource supply is low, resilience is expected to be low and resistance is likely to be the dominant property of the community. Average biomass and peak biomass are expected to be low in such habitats (Fig. 8.1). Thus theoretical considerations suggest that community resilience should be controlled by a combination of disturbance frequency and resource supply.

A number of laboratory studies have explored these flood disturbance - resource supply interactions. De Angelis et al. (1990) found that periphyton in low nutrient, laboratory streams were less resistant to a single scour disturbance than those in moderate nutrient streams, supporting the concept that nutrient supply may have important effects on system resistance. Mulholland et al. (1991) found that snail grazing increased resistance to a scour disturbance by removing loosely adhering taxa, thus maintaining a dominance of low-profile, tightly adhering species with high disturbance resistance. However, they found that nutrient supply alone had little effect on resistance, and the effect of increased nutrient supply on resilience was only positive if grazers were present. Several studies on disturbance - resource interactions have also been reported from natural streams. Grimm and Fisher (1989) concluded that resistance of periphyton in their Sonoran desert stream was a function of community growth form and mode of attachment, but that resilience was primarily a function of nutrient inputs and season. Fisher and Grimm (1988) also demonstrated that disturbance frequency did not explain significant variance in periphyton biomass in an unenriched river draining a forested watershed, but that it did in a more enriched Sonoran desert stream. Similarly, I found (Chapter 2) that mean monthly periphyton biomass across a broad spectrum of New Zealand streams was strongly correlated with flood disturbance parameters at sites with moderate and high nutrient supplies, but was not related to these parameters at sites with low nutrient supplies. At the latter sites, periphyton resilience was sufficiently low so that the next disturbance had little effect (i.e., resistance was high).

In this chapter, I describe an experiment to examine in detail the effects of resource supply on resistance and resilience of stream periphyton to a single

disturbance. I then examine the results in relation to the disturbance - resource supply - grazer concept described in Chapter 6. I hypothesized that: a) under conditions of low light and low nutrient resources, periphyton communities would have low resistance and resilience to disturbance with average biomass during the recovery phase primarily reflecting community resistance (i.e., percentage of biomass remaining after disturbance); and b) under high light and high nutrients community resistance would also be low, but post-disturbance resilience would be high and average biomass during the recovery phase would primarily reflect this resilience. The study was performed in large outdoor experimental streams at the University of Michigan Biological Station experimental stream facility, near Pellston, Michigan, USA.

## II. Methods

*Experimental design.*

I used eight non-recirculating artificial streams that were constructed from untreated wood sealed with polyurethane. Each stream was 3.5 m long and 25.5 cm wide. The artificial streams were fed with natural stream water pumped from the east branch of the Maple River (a third order river draining mesotrophic Douglas Lake) at a rate of 1.5 L/s/trough. Gradients of the streams were adjusted to attain an average depth of 2 cm (+/- 0.2 cm) and an average velocity of 30 cm/s.

A two-stage, 90 cm long, mixing and settling compartment was present at the head of each stream. The depth of water within this compartment was maintained at 12 cm by a barrier dam at the downstream end. Water was delivered under pressure to the head of the compartment creating considerable turbulence. Twenty centimeters downstream of the entry point I placed three columnators (i.e., flow straighteners); each 2 cm wide, spaced 7 cm apart, and made from twin sheets of plastic lighting grate. These functioned to remove medium and large-scale eddies from the flow. The water then entered a 50 cm long settling pool which trapped most of the incoming sediment and detritus. Water flowed over the downstream barrier dam for 20 cm before going through another set of three columnators to create parallel flow in the experimental section. The 2.8 m long experimental section was lined with 4.8 $cm^2$, unglazed, ceramic tiles (100% cover of the trough bottom) to serve as substrata for the periphyton.

The resource conditions under which the periphyton grew were manipulated by altering light levels (high and low) along half of the streams and by adding nutrients to four of the streams to produce four treatments in a 2 x 2 factorial design (with 4 replicates per treatment). In summary the treatments were: high light, high nutrients (HL, HN); high light, low nutrients (HL, LN); low light, high nutrients (LL, HN); and low light, low nutrients (LL, LN). Low light levels were achieved by covering half of each stream (alternating upstream/downstream for each stream) with neutral density filters (Calumet Co., Bensonville, IL 60106, USA). These reduced ambient photon flux density by approximately 75% with light intensities on cloudless days on the underlying substratum of 100 - 200 umol/$m^2$/s at mid-morning rising to a one hour peak of 400 umol/$m^2$/s in the early afternoon, before dropping again. This range in light intensities was very similar to that reported by DeNicola et al. (1992) for a North American stream shaded by black willow (*Salix nigra*). Natural light levels were so high during early afternoon (typically exceeding 1500 - 1800 umol/$m^2$/s) that there was concern that photoinhibition could occur in the communities if natural sunlight was used for the high light treatment (e.g., Boston and Hill 1991). Thus, a layer of shade cloth was used in these sections of the troughs to reduce ambient light by 40 % and produce maximum light intensities of 1000 - 1200 umol/$m^2$/s. This is similar to intensities for open streams near mid-day (DeNicola et al. 1992). Maximum daily water temperatures were as high as 23 $^{o}$C with diel variation rarely exceeding $\pm$ 3 $^{o}$C.

For the nutrient treatment, $NaH_2PO_4$ and $NaNO_3$ solutions were dripped into the turbulent zone of the header compartments of the four high nutrient streams using peristaltic pumps. Target nutrient concentrations were 30 ppb soluble reactive phosphorus (SRP) and 300 ppb $NO_3$-N. Average concentrations measured in the streams on 2 occasions were 22 ppb SRP and 188 ppb $NO_3$-N. The non-enriched streams served as the low nutrient treatment with 6 ppb SRP and 19 ppb $NO_3$-N. Data from other experiments at the research facility over my experimental period indicated high stream inflow concentrations of ammonia and that phosphorus was limiting periphyton growth (R. J. Stevenson, unpublished data). A comparison of growth in the low nutrient treatment streams at 6 ppb SRP with that for a similar $PO_4$-P concentration reported by Bothwell (1989) also suggested low bioavailability of SRP in the inflow waters. In the high nutrient treatment, inflow $PO_4$-P concentrations were based on the results of Bothwell (1989) who found that maximum areal biomass for diatoms reached an assymptote at 30 ppb SRP for P-limited communities.

The experiment began on 16 July 1993 with an initial 8 d period of colonization with light treatments in place, but no added nutrients. On Day 8 the nutrient treatment was started in four of the streams and continued for the remainder of the experiment. Pre-disturbance sampling of periphyton was completed on Day 15. On Day 18, while the enriched communities were still in the middle of their exponential growth phase, a set of 18 tiles (3 rows of 6 tiles) was removed from the downstream end of each stream and held in a bucket containing water from the treatment from which they were removed. Dummy tiles were placed in the streams to fill in the gaps to maintain the roughness configuration of the bed. All streams were then subjected to a standardized scour disturbance to simulate a spate. The single disturbance consisted of increasing the flow and slope of each stream for 30 minutes, so that water velocities were increased to 45 - 55 cm/s (measured using hot-film anemometry). I then gradually released 6 L of river gravels (mean breadth dimension = 3.1 cm), which took approximately 5 minutes, during the period of elevated flows. These gravels tumbled down the stream to simulate abrasion by bed movement. A mesh grate at the downstream end of each stream collected the gravels so that the same bed materials could be used in all replicate streams. The original flow conditions were resumed at the end of the 30 minute disturbance. The set of 18 undisturbed substrata were then returned to their respective streams. These tiles served as a control and enabled me to evaluate the effects of the disturbance on longer-term community dynamics compared with the dynamics of that community had it not been disturbed (e.g., growth rates of the disturbed vs. undisturbed communities, rates of succession in disturbed vs. undisturbed communities, degree of biomass and taxonomic re-set caused by the disturbance) for the four resource treatments. An immediate post-disturbance sampling of the impacted tiles was then carried out. Further post-disturbance sampling of both undisturbed (control) and disturbed tiles was undertaken on Days 20, 23 and 27 of the experiment.

Few invertebrates were observed in the channels during the course of the experiment so grazing aspects of the disturbance-resource supply-grazer model could not be considered.

*Analytical.*

On Days 15 and 18 the following parameters were measured: ash-free dry mass (AFDM), chlorophyll *a*, percentage chlorophyll *a*, gross primary production (GPP), community respiration (CR), percentage periphyton carbon (% C), percentage periphyton nitrogen (%N) and relative abundance of taxa. The post-disturbance accrual phase samples were analysed for AFDM, chlorophyll *a* and the relative

abundance of taxa. All samples were obtained by removing a row of 4 tiles from near the downstream end of each treatment and brushing the periphyton community from them. New dummy tiles were placed in their positions to maintain the previous near-bed flow characteristics. Rows were removed consecutively up-stream for subsequent samplings to minimize sampling disturbance to unsampled tiles. No longitudinal variation in periphyton cover was observed over the sampling sections.

Community metabolism was determined while the periphyton were still attached to the tiles using a rapid dissolved oxygen-respirometry method (Hickey 1988). For this, the set of 4 sampling tiles per stream was placed around the perimeter of a circular plexiglass chamber (1.29 L) with a central stirring bar and with the upstream edge of the tile facing into the direction of the current. A lid, with a YSI dissolved oxygen probe inserted through it, was then placed on the stream water-filled chamber (ensuring that no free air was trapped inside), with a 1cm deep layer of water on top to further isolate the lid from the atmosphere. Petroleum jelly was also applied to help seal the lid. All incubations were completed outdoors during cloudless conditions from 11 am to 3 pm. At the beginning of the incubations a shade filter, appropriate to the treatment from which the tiles had been obtained, was placed over the chamber and water current was generated by activating the stirring bar (to half of full scale). Changes in oxygen over a 10 minute incubation period were monitored by routing the milli-volt output from the dissolved oxygen meter through an electronic scale expander to subtract the starting oxygen concentration and expand a 1 mg/L working range to full scale. Changes in oxygen concentration with a precision of 0.005mg/L were displayed on a chart recorder. Linear kinetics were generally achieved within 2 - 5 minutes of the commencement of each incubation and the gradient of the chart line was used to calculate net primary production (NPP). Once sufficient record had been obtained (approximately 5 minutes), the chamber was covered with an opaque rubber sheet. Within minutes the dissolved oxygen trajectory became negative and the linear portion of the curve was used to calculate community respiration (CR). Both NPP and CR were corrected for changes in temperature during the incubations. Gross primary production (GPP) was calculated as the sum of NPP and CR. Following the determination of community metabolism, the periphyton was brushed from the tiles into a container, homogenized using a blender, and sub-sampled for various further analyses.

The relative abundance of taxa was determined by analyzing wet mounts at 900 X magnification using random fields, with separate counts of live (chlorophyll bearing) and dead (non-chlorophyll bearing) taxa. Over 300 cells (or filaments for

small cyanobacteria) were enumerated for each sample. AFDM was determined gravimetrically after drying for 24 hr at 105°C and combusting for 1hr at 500 °C. Chlorophyll *a* was determined spectrophotometrically using boiling (78 °C) 90% ethanol as extractant, correcting for phaeopigments by acidification, and employing a chlorophyll *a* coefficient of 28.66 (Sartory and Grobelaar 1985). A measure of the percentage of the mat composed of chlorophyll *a* was calculated as chlorophyll *a* divided by AFDM (both in mg) x100.

Percentage cellular carbon and nitrogen were determined on subsamples dried for 24 hr at 105 °C and analysed on a Perkin-Elmer 2400 CHN elemental analyzer. Mat bulk density for the undisturbed communities on Day 23 (time of peak biomass in the high resource communities) was estimated by measuring mat thickness of 4 tiles from each treatment using fine scale vernier calipers. Sample dry weights were divided by their original thickness to obtain bulk density.

*Data analysis.*

Data analysis consisted of two parts: first, analysis of resistance and resilience as a function of resource supply; and second, determining what effects the disturbance had on longer term temporal biomass dynamics and successional trajectories for the different treatments. Resistance was thus determined as relative biomass loss calculated as the percentage change in AFDM and chlorophyll *a* between the pre- and post-disturbance communities for the day of the disturbance (Day 18). The pre-disturbance values were estimated from the growth rate of the undisturbed communities. Percentage biomass loss is a fundamental, and widely used, measure of the degree of scour (and thus resistance) by flood disturbances (e.g., Biggs and Close 1989, Grimm and Fisher 1989, Mulholland et al. 1991, Peterson and Stevenson 1992). Resilience was determined in two ways: as the mean exponential rate of increase in chlorophyll *a* ( i.e., growth rate, *r*), and as nominal time to recover to the pre-disturbance chlorophyll *a* concentration ($T_r$) (alternatively called $T_S$; Mulholland et al. 1991). Growth rate (*r*) is probably a better measure of resilience if disturbance results in equal displacement of the community. However, if differential resistance occurs, resulting in different starting points, then $T_r$ is probably a better measure (Mulholland et al. 1991).

The degree to which the disturbance altered overall community development was determined by comparing biomass, growth rates and successional trajectories over time, between the disturbed and undisturbed (control) communities. This provided a measure of the relative contribution of individual disturbances to longer term

temporal dynamics of the periphyton. It also gives an absolute basis for determining the disturbance effects, rather than just an inter-treatment comparison as has been done in the past (e.g., Mulholland et al. 1991). The degree of biomass reset was estimated from graphical interpolation of the number of days back in the accrual curve when that same AFDM and chlorophyll *a* biomass had been recorded.

AFDM and chlorophyll *a* data were log transformed prior to ANOVA to achieve homogeneity of variances. All other parameters were untransformed. The significance and degree of interaction of the disturbance, light, and nutrients on all community parameters was then determined using Day 15 (pre-disturbance) and Day 18 (post-disturbance) data sets and a 3-way ANOVA (with four replicates per treatment).

Disturbed and undisturbed community growth rates were calculated using changes in chlorophyll *a* versus time from a power-law model (chlorophyll $a = ae^{rT}$) and linear regression, where T represents days of accrual (Bothwell 1988). Standard error values were used for calculating 95% confidence intervals(Students $t_{(n-1\ d.f.)}$ x S.E.). These were then used to determine the significance of differences in *r* between disturbed and undisturbed communities (on the criterion that the 95% C.I. of one did not overlap *r* for the other treatment).

Changes in community structure during accrual, with and without disturbance, were assessed using principal components analysis. Factor scores were calculated for each treatment based on the relative abundance of the 8 most common taxa. Values for the first two factors were averaged for each treatment per sampling occasion and used as coordinates to identify changes in the undisturbed and disturbed successional trajectories over time. All statistical analyses and plotting were carried out using SYSTAT/SYGRAPH (Wilkinson 1991).

## III. Results

*General.*

There was a slow rate of periphyton accrual under ambient (control) nutrient conditions, regardless of the light treatment (Fig. 8.2a,b). These low nutrient treatment communities had high AFDM relative to chlorophyll *a* (usually 0.1 - 0.3 % chlorophyll *a*). Much of the mat was non-phototrophic allochthonous fine particulate organic matter. The addition of nutrients on Day 8 to half the troughs greatly

stimulated accrual of AFDM and chlorophyll *a* under both light treatments. Peak biomass occurred in the low nutrient treatments on Day 15, but did not occur until eight days later (Day 23) in the high nutrient treatments.

There were significant differences in the colonization and initial growth of the communities as a function of resource treatments by Day 15 (Tables 8.1 and 8.2). Light alone had no effect on any of the variables, but nutrients moderately stimulated AFDM accrual, chlorophyll specific GPP, chlorophyll *a* per cell, and strongly stimulated chlorophyll *a* concentrations, areal GPP, community respiration, density of live cells, number of dead cells in the mat, % chlorophyll *a*, % carbon, and % nitrogen. Conversely, it also significantly reduced C:N ratios. These responses indicated that the communities were more limited by nutrients than light in this experiment. However, there was a strong interaction between nutrients and light for chlorophyll *a* (and % chlorophyll *a*) resulting in chlorophyll concentrations that were over twice as high by Day 15 under LL, HN than with HL, HN (Table 8.1). These effects were clearly visible in terms of macroscopic community structure with the HL, HN communities being relatively loosely aggregated and the LL, HN communities, being much darker, denser and more cohesive. These differences became even more accentuated in the undisturbed communities later in the accrual cycle. At the time of peak biomass for the undisturbed community (Day = 23), relative differences in bulk density were large (Fig. 8.3). The low light, low and high nutrient communities had higher bulk densities than their paired high light equivalents. While the reduction of light increased bulk density, the addition of nutrients compounded this effect. Thus, both nutrients and light had highly significant, but independent, effects on mat bulk density.

Major differences in the rate of growth were found during the exponential phase of the accrual curve in high nutrient treatments (Fig. 8.2a,b; Table 8.3). While colonization and initial accrual to Day 15 were twice as high under LL, HN (Table 8.1), growth during the next phase (to Day 23) was almost twice as high under the HL, HN treatment. However, by Day 23 when peak biomass occurred in both nutrient enriched light treatments there was no significant difference in chlorophyll *a* concentration (or AFDM) ($p > 0.05$, t-test) between the treatments. Chlorophyll *a* concentration in both enriched high and low light treatments decreased after Day 23. The loss was significantly greater under low light ($p = 0.016$, t-test).

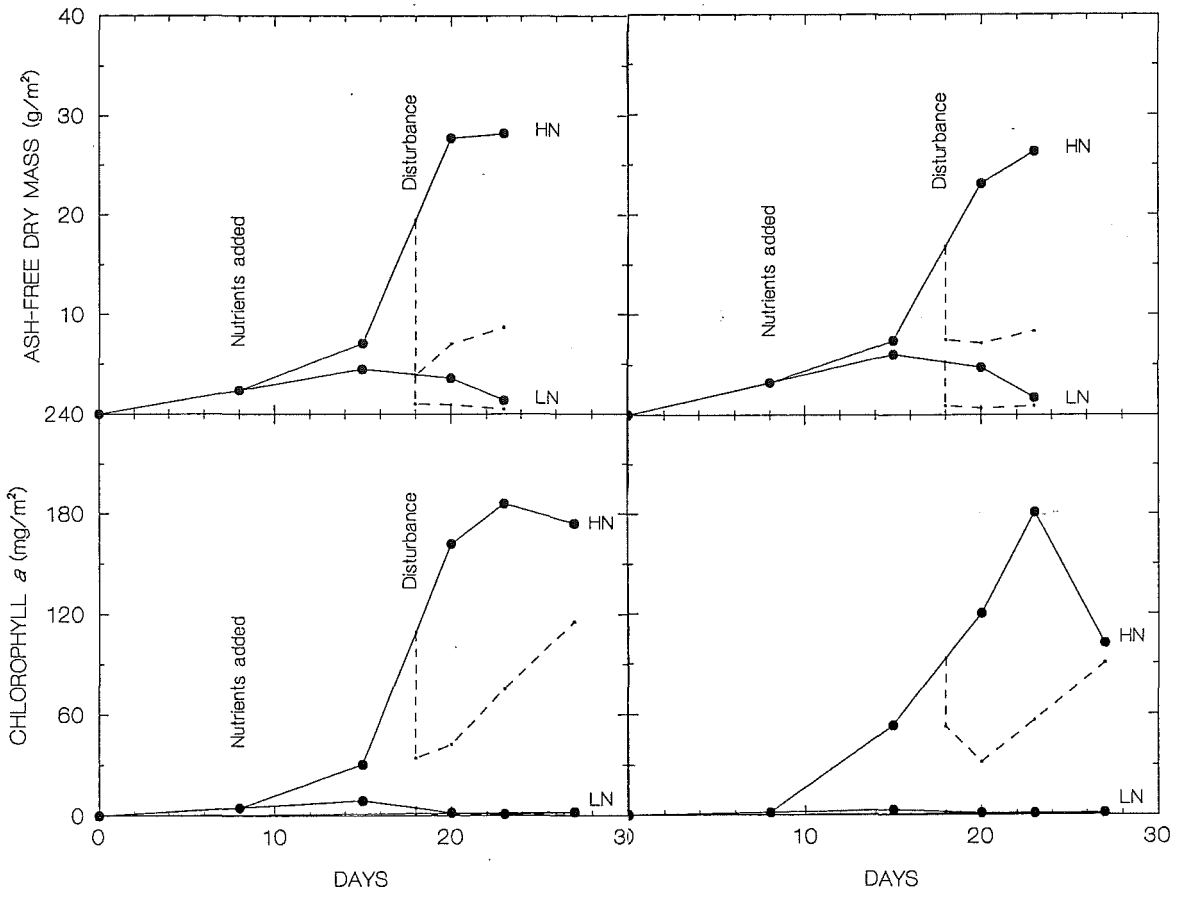


Fig. 8.2: AFDM and chlorophyll *a* dynamics of the a) high light treatment, and b) low light treatment during the study. The solid line represents the undisturbed community, the dashed line represents the disturbed community (HN, high nutrients; LN, low nutrients). Values are calculated as geometric means. Error bars are omitted for clarity. See Table 8.1 for standard errors for Day 15 undisturbed, and Day 18 disturbed, communities.

**TABLE 8.1.** Summary of mean pre- and post-disturbance community parameters for each experimental treatment (HL, HN = high light, high nutrients; HL, LN = high light, low nutrients; LL, HN = low light, high nutrients; LL, LN = low light, low nutrients).

| | Pre-disturbance (Day 15) | | | | Post-disturbance (Day 18) | | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | HL HN | HL LN | LL HN | LL LN | HL HN | HL LN | LL HN | LL LN |
| Live cells (no. $mm^{-2}$) | 56 | 1.2 | 37 | 0.87 | 46 | 2.2 | 28 | 1.1 |
| S.E. | 24 | 0.28 | 12 | 0.17 | 13 | 0.4 | 3.3 | 0.5 |
| Dead cells (no. $mm^{-2}$) | 5.0 | 0.3 | 1.8 | 0.17 | 2.4 | 0.75 | 1.3 | 0.48 |
| S.E. | 2.7 | 0.06 | 0.51 | 0.03 | 1.1 | 0.09 | 0.2 | 0.18 |
| Dead:live cells | 0.066 | 0.279 | 0.05 | 0.218 | 0.050 | 0.360 | 0.048 | 0.488 |
| S.E. | 0.018 | 0.024 | 0.01 | 0.020 | 0.016 | 0.026 | 0.012 | 0.092 |
| AFDM ($g.m^{-2}$) | 7.3 | 4.7 | 7.7 | 4.3 | 4.3 | 1.1 | 7.6 | 0.8 |
| S.E. | 1.00 | 0.83 | 1.16 | 2.10 | 1.3 | 0.14 | 0.8 | 1.13 |
| Chlorophyll *a* ($mg.m^{-2}$) | 25 | 9.6 | 57 | 3.6 | 38 | 0.4 | 53 | 0.8 |
| S.E. | 8.3 | 5.6 | 12 | 1.3 | 9.91 | 0.01 | 2.9 | 0.38 |
| % Chlorophyll *a* | 0.35 | 0.22 | 0.72 | <0.01 | 0.93 | 0.03 | 0.72 | 0.08 |
| S.E. | 0.098 | 0.146 | 0.038 | 0.173 | 0.132 | 0.002 | 0.081 | 0.07 |
| Chlorophyll *a* per cell (ng) | 1.03 | 2.93 | 2.00 | 2.86 | 1.05 | 1.6 | 1.98 | 1.57 |
| S.E. | 0.75 | 1.80 | 0.52 | 0.61 | 0.34 | 0.20 | 0.33 | 1.02 |
| GPP (mg $0_2.m^{-2}.hr^{-1}$) | 305 | 22 | 345 | 12 | 309 | 32 | 360 | 40 |
| S.E. | 35 | 5.3 | 13.8 | 5.6 | 26 | 4 | 48 | 6 |
| GPP (mg $0_2$.mg chl.*a*.$hr^{-1}$) | 25 | 3.2 | 6.7 | 5.7 | 9.5 | - | 6.8 | - |
| S.E. | 15 | 1.3 | 1.1 | 3.6 | 1.7 | - | 0.8 | - |
| CR (mg $0_2.m^{-2}.hr^{-1}$) | 122 | 81 | 116 | 57 | 70 | 16 | 86 | 17 |
| S.E. | 9 | 25 | 8 | 10 | 8 | 8 | 13 | 10 |
| Carbon (%) | 13 | 11 | 16 | 11 | 17 | 15 | 20 | 16 |
| S.E. | 1.6 | 0.80 | 0.44 | 1.19 | 2.4 | 3.4 | 1.1 | 2.8 |
| Nitrogen (%) | 1.3 | 0.82 | 1.7 | 0.85 | 1.5 | 1.3 | 2.2 | 1.6 |
| S.E. | 0.29 | 0.08 | 0.20 | 0.13 | 0.24 | 0.26 | 0.30 | 0.27 |
| C:N | 10.0 | 14.0 | 9.95 | 13.90 | 11.5 | 11.9 | 9.5 | 10.3 |
| S.E. | 0.95 | 0.75 | 0.94 | 0.97 | 1.08 | 0.22 | 1.09 | 0.47 |

**TABLE 8.2.** Analysis of variance of the effects of light levels and nutrients (two levels for each parameter) on the periphyton communities on Day 15 (pre-disturbance).

| | Source | S.S. | D.F. | F ratio | *P* |
|---|---|---|---|---|---|
| 1: | AFDM | | | | |
| | Light (L) | 0.001 | 1 | 0.000 | 0.993 |
| | Nutrients (N) | 36.000 | 1 | 4.888 | 0.047 |
| | L x N | 0.627 | 1 | 0.085 | 0.775 |
| | Error | 88.332 | 12 | | |
| 2: | Chlorophyll *a* | | | | |
| | Light (L) | 667.951 | 1 | 2.833 | 0.118 |
| | Nutrients (N) | 4720.977 | 1 | 20.023 | 0.001 |
| | L x N | 1419.703 | 1 | 6.021 | 0.030 |
| | Error | 2829.341 | 12 | | |
| 3: | GPP (areal) | | | | |
| | Light (L) | 843.483 | 1 | 0.524 | 0.484 |
| | Nutrients (N) | 350,403.734 | 1 | 217.787 | 0.000 |
| | L x N | 2,286.631 | 1 | 1.421 | 0.258 |
| | Error | 17,698.244 | 11 | | |
| 4: | Ln GPP (chlorophyll specific) | | | | |
| | Light (L) | 0.558 | 1 | 0.42 | 0.517 |
| | Nutrients (N) | 6.555 | 1 | 5.315 | 0.044 |
| | L x N | 0.787 | 1 | 0.638 | 0.443 |
| | Error | 12.333 | 10 | | |
| 5: | CR | | | | |
| | Light (L) | 870.593 | 1 | 0.998 | 0.337 |
| | Nutrients (N) | 9950.063 | 1 | 11.409 | 0.005 |
| | L x N | 295.160 | 1 | 0.338 | 0.571 |
| | Error | 10,465.523 | 12 | | |
| 6: | Ln Dead cells | | | | |
| | Light (L) | 0.640 | 1 | 0.650 | 0.439 |
| | Nutrients (N) | 15.538 | 1 | 15.770 | 0.003 |
| | L x N | 0.043 | 1 | 0.043 | 0.839 |
| | Error | 9.853 | 10 | | |
| 7: | % Chlorophyll *a* | | | | |
| | Light (L) | 0.019 | 1 | 0.475 | 0.504 |
| | Nutrients (N) | 0.745 | 1 | 18.951 | 0.001 |
| | L x N | 0.370 | 1 | 9.412 | 0.010 |
| | Error | 0.472 | 12 | | |

| | Source | S.S. | D.F. | F ratio | *P* |
|---|---|---|---|---|---|
| 8: | % Carbon | | | | |
| | Light (L) | 9.976 | 1 | 2.578 | 0.137 |
| | Nutrients (N) | 32.214 | 1 | 8.323 | 0.015 |
| | L x N | 7.564 | 1 | 1.954 | 0.190 |
| | Error | 42.575 | 11 | | |
| 9: | % Nitrogen | | | | |
| | Light (L) | 0.112 | 1 | 0.973 | 0.345 |
| | Nutrients (N) | 1.588 | 1 | 13.799 | 0.003 |
| | L x N | 0.077 | 1 | 0.667 | 0.431 |
| | Error | 1.266 | 11 | | |
| 10: | C:N | | | | |
| | Light (L) | 0.013 | 1 | 0.949 | 0.651 |
| | Nutrients (N) | 57.552 | 1 | 0.001 | 0.000 |
| | L x N | 0.000 | 1 | 1.000 | 0.054 |
| | Error | 34.048 | 11 | | |
| 11: | Ln Chlorophyll per cell | | | | |
| | Light (L) | 0442 | 1 | 0.527 | 0.486 |
| | Nutrients (N) | 4.947 | 1 | 5.893 | 0.036 |
| | L x N | 1.795 | 1 | 2.139 | 0.178 |
| | Error | 7.556 | 9 | | |
| 12: | Ln Bulk density (Day 23) | | | | |
| | Light (L) | 3.053 | 1 | 32.805 | 0.000 |
| | Nutrients (N) | 22.473 | 1 | 241.464 | 0.000 |
| | L x N | 0.214 | 1 | 2.296 | 0.156 |
| | Error | 1.117 | 12 | | |
| 13: | *Achnanthidium minutissimum* | | | | |
| | Light (L) | 15.388 | 1 | 0.215 | 0.651 |
| | Nutrients (N) | 2697.808 | 1 | 37.672 | 0.000 |
| | L x N | 326.235 | 1 | 4.556 | 0.054 |
| | Error | 859.348 | 12 | | |
| 14: | *Gomphonema* sp. | | | | |
| | Light (L) | 44.166 | 1 | 0.951 | 0.349 |
| | Nutrients (N) | 92.513 | 1 | 1.991 | 0.184 |
| | L x N | 59.944 | 1 | 1.290 | 0.278 |
| | Error | 557.500 | 12 | | |
| 15: | *Schizothrix calcicola* | | | | |
| | Light (L) | 17.160 | 1 | 12.609 | 0.004 |
| | Nutrients (N) | 1.864 | 1 | 1.370 | 0.265 |
| | L x N | 2.486 | 1 | 1.826 | 0.201 |
| | Error | 16.332 | 12 | | |

| | Source | S.S. | D.F. | F ratio | *P* |
|---|---|---|---|---|---|
| 16: | *Fragilaria* sp. | | | | |
| | Light (L) | 41.212 | 1 | 2.393 | 0.148 |
| | Nutrients (N) | 249.984 | 1 | 14.516 | 0.002 |
| | L x N | 34.887 | 1 | 2.026 | 0.180 |
| | Error | 206.656 | 12 | | |
| 17: | *Navicula* sp. | | | | |
| | Light (L) | 0.192 | 1 | 0.601 | 0.453 |
| | Nutrients (N) | 0.075 | 1 | 0.235 | 0.637 |
| | L x N | 0.203 | 1 | 0.635 | 0.441 |
| | Error | 3.836 | 12 | | |

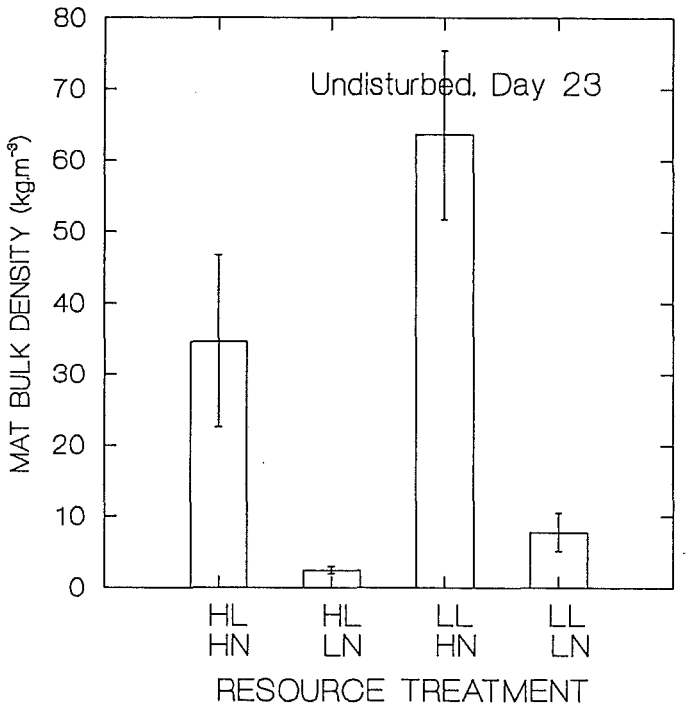


Fig. 8.3: Mat bulk density of the undisturbed communities on Day 23 (HL, HN: high light, high nutrients; HL, LN: high light, low nutrients; LL, HN: low light, high nutrients; LL, LN: low light, high nutrients).

TABLE 8.3 Summary of overall periphyton growth rates ($r$) and S.E. for undisturbed communities, and $T_r$ (days to recover to pre-disturbance chlorophyll *a* concentration) as a function of light and nutrient treatments.

| Resource treatment | Disturbance treatment | Data used Days | $r$ | SE | $T_r$ Days |
|---|---|---|---|---|---|
| High light, high nutrients | undisturbed | 15, 20, 23 | 0.238 | 0.077 | 5.9 |
| | disturbed | 20, 23, 27 | 0.142 | 0.024 | |
| High light, low nutrients | undisturbed | 0, 15 | 0.117 | 0.047 | >18 |
| | disturbed | 20, 23, 27 | 0.022 | 0.040 | |
| Low light, high nutrients | undisturbed | 15, 20, 23 | 0.153 | 0.007 | 6.0 |
| | disturbed | 20, 23, 27 | 0.148 | 0.022 | |
| Low light, low nutrients | undisturbed | 0, 15 | 0.095 | 0.018 | >18 |
| | disturbed | 20, 23, 27 | 0.010 | 0.003 | |

The structure of the communities did not vary greatly as a function of resource treatments. By Day 15 the communities in all treatments were dominated by diatoms with *Achnanthidium minutissimum* comprising 78 - 93% of the total cells (Fig. 8.4). The assemblages also contained subdominant populations of *Gomphonema* spp., *Fragilaria* spp., *Navicula* spp., and *Schizothrix calcicola.* Nutrient addition, but not light intensity, had a significant stimulatory effect on the relative abundance of *Achnanthidium* and *Fragilaria. Achnanthidium* was stimulated by nutrients more than the other taxa. Conversely, *Schizothrix* had a significantly higher relative abundance under low light, but did not respond to nutrients (Table 8.2).

The same suite of taxa continued to dominate through Day 27 of the experiment (Fig. 8.4). However, there was a slight reduction in the relative abundance of *Achnanthidium* over the accrual cycle, especially for the HL, HN treatments. *Spirogyra* sp. was observed in the channels as small, isolated tufts, but it never grew to significant levels. This is thought to be a function of the moderate - high velocities in the channels since they are particularly prone to shear stress displacement (see Chapter 3).

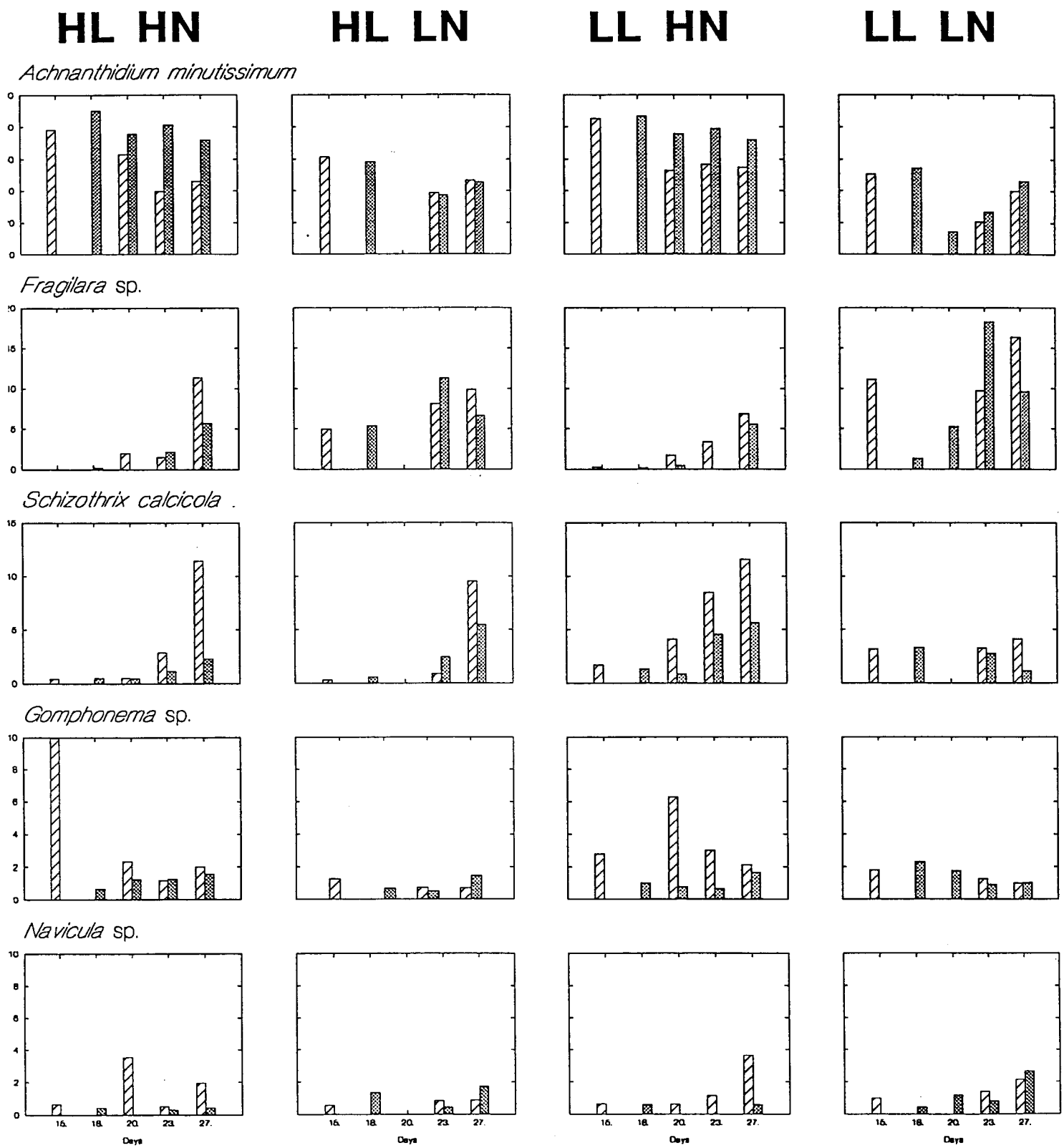


Fig. 8.4: Relative abundance of *Achnanthidium minutissimum*, *Fragilaria* sp., *Schizothrix calcicola*, *Gomphonema* sp., and *Navicula* sp. in the undisturbed communities at four time intervals during the accrual cycle (hatched bars denoted disturbed communities; see Fig. 8.3 for definition of resource treatment abbreviations).

*Resistance as a function of resource supply*

There were considerable differences in resistance as a function of resource supply. Overall, AFDM was less resistant than chlorophyll *a* in three of the four resource treatments (Table 8.4). Percentage AFDM loss was similar between the HL, HN and LL, LN treatments. However, loss was only moderate in the LL, HN treatment suggesting that the total organic matter of this community had a much greater resistance to scour disturbance. Similarly, resistance of the autotrophic component, as measured by change in chlorophyll *a*, was greatest under the LL, HN treatment. Communities in the HL, LN treatment had the lowest resistance with over 90% of chlorophyll *a* being lost with the disturbance.

**TABLE 8.4** Summary of percentage loss of ash-free dry mass and chlorophyll *a*, and number of days in the accrual cycle that these variables were set back (reset) for the periphyton communities under four treatments following disturbance. Comparisons were based on interpolation of values between Day 15 and 20 for the undisturbed communities.

| | Resource treatment | | % loss AFDM | % loss Chlorophyll *a* | Days reset AFDM | Days reset Chlorophyll *a* |
|---|---|---|---|---|---|---|
| 1 | High light, high nutrients | $\bar{x}$ | 77 | 68 | 8 | 3 |
| | | S.E. | 6.7 | 5.1 | - | - |
| 2 | High light, low nutrients | $\bar{x}$ | 74 | 94 | 14.5 | 16 |
| | | S.E. | 2.7 | 2.9 | - | - |
| 3 | Low light, high nutrients | $\bar{x}$ | 54 | 43 | 3 | 8 |
| | | S.E. | 7.4 | 7.0 | - | - |
| 4 | Low light, low nutrients | $\bar{x}$ | 64 | 82 | 16 | 16 |
| | | S.E. | 20.6 | 3.9 | - | - |
| ANOVA *P*-values resource treatment | | | 0.115 | 0.007 | - | - |
| Covariate (initial biomass) | | | 0.046 | 0.786 | - | - |

Biomass of the communities (both as AFDM and chlorophyll *a*) was significantly affected by disturbance and nutrients, with the interaction term between treatments also being significant (Table 8.5). The light x nutrient and disturbance x light x nutrient interaction terms were also significant for chlorophyll *a* suggesting that both light and nutrient supply were limiting factors, and that the effects of disturbance depends on both resources. Some of these biomass results were reinforced by analysis of metabolism (Table 8.1). The disturbance and, particularly, nutrients generally increased areal and chlorophyll specific GPP (Table 8.1, 8.6). Nutrients also increased CR, but disturbance decreased it significantly. The disturbance also caused a major reduction in chlorophyll *a* concentration per cell in the unenriched treatments. Whereas there was a major loss of the autotrophic component with disturbance, the relative reduction in the heterotrophic community (as indicated by CR) was much greater, particularly in the low nutrient treatments. The disturbance also caused a major increase in chlorophyll-specific GPP (Tables 8.1,

8.6) and reduction in density of dead cells in the enriched treatments (disturbance x nutrient interaction, $p = 0.040$). These results suggest that the disturbance freed the community of detritus (dead cells and perhaps fine particulate organic matter) which may have been absorbing light and retarding photosynthetic activity in the thin film of the low nutrient treatment communities.

Disturbance also had a significant effect on other community attributes. Percentage chlorophyll *a* increased strongly in the high light communities (but not under low light) following the disturbance (Table 8.1). The disturbance x nutrient, and disturbance x nutrient x light interaction terms were all significant (Table 8.5). The percentage carbon in the mat increased strongly as a result of the disturbance, but did not respond to resource treatments. Percentage nitrogen also increased as a result of the disturbance (and nutrient addition, as noted earlier), but there were no interactive effects with either light or nutrients. However, there was a significant interactive effect between disturbance and nutrients for C:N ratios: the disturbance caused much higher C:N ratios in the low nutrient treatments indicating that the disturbance improved the physiological status of these communities.

The disturbance had no significant effect on the relative abundance of the 5 most common taxa (Tables 8.7, Fig. 8.4). Consistent with the pre-disturbance analysis, nutrients had a significant, stimulatory, effect on the relative abundance of *Achnanthidium.* However, *Fragilaria* had higher relative abundance under low nutrients and *Schizothrix* had higher relative abundance under low light. Disturbance and nutrients had a significant interactive effect on the relative abundance of *Fragilaria.*

**TABLE 8.5** F-ratios from an analysis of variance of the effects of the disturbance (comparison of the pre-disturbance Day 15 communities with those after the disturbance on Day 18), light intensity, and nutrients (two levels for each parameter) on periphyton mass parameters (* = $P$ <0.05, ** = $P$ <0.01, *** = $P$ <0.001).

| | ANOVA F-ratios | | | | | |
|---|---|---|---|---|---|---|
| Source | AFDM | Chl.*a* | %Chl.*a* | %C | %N | C:N |
| Disturbance (D) | 19.2*** | 17.3*** | 3.1 | 8.0** | 7.6* | 3.5 |
| Light (L) | 0.9 | 0.7 | 0.0 | 1.6 | 4.2 | 2.4 |
| Nutrients (N) | 20.3*** | 160.0*** | 77.3*** | 4.1 | 10.9** | 13.9*** |
| D x L | 0.0 | 0.8 | 1.2 | 0.0 | 1.0 | 2.1 |
| D x N | 9.4** | 28.2*** | 6.0* | 0.0 | 0.5 | 7.6** |
| L x N | 0.4 | 4.5* | 1.6 | 0.8 | 1.1 | 0.0 |
| D x L x N | 1.4 | 4.4* | 10.2** | 0.0 | 0.3 | 0.0 |

**TABLE 8.6** F-ratios for an analysis of variance of the effects of disturbance (comparison of the pre-disturbance Day 15 communities with those after the disturbance on Day 18), light intensity, and nutrients (two levels for each parameters) on periphyton metabolism (* = $P$ <0.05, ** = $P$ <0.01, *** = $P$ <0.001).

| | ANOVA F-values | |
|---|---|---|
| Source | GPP. $m^{-2}$ | CR |
| Disturbance (D) | 7.3* | 15.3*** |
| Light (L) | 0.7 | 0.1 |
| Nutrients (N) | 166.8*** | 20.6*** |
| D x L | 2.7 | 0.1 |
| D x N | 6.7* | 6.2* |
| L x N | 2.1 | 0.2 |
| D x L x N | 2.7 | 0.1 |

*Resilience as a function of resource supply.*

Resilience of the communities varied greatly as a function of resource supply measured both as $r$ and $T_r$. A two day delay followed the disturbance before growth resumed in the high nutrient treatments (high and low light) (Fig. 8.2 a,b). The residual, post-disturbance, biomass was approximately equivalent to that of the undisturbed communities at the end of initial colonization (i.e., Day 15), and growth kinetics thereafter were linear suggesting that this residual biomass was largely viable. While both high nutrient treatments had similar, relatively high, growth rates (Table 8.3), the HL, LN treatment had a rate only 15% of its high nutrient equivalent, and the LL, LN treatment had a rate that was only half this again. The differences between these three rates were all significant ($p < 0.05$). By the conclusion of the experiment, chlorophyll *a* had returned to the Day 18, pre-disturbance, level in the high nutrient treatments, but not in the low nutrient treatments. Thus, there was a significant difference in $T_r$ ($p = 0.005$, Kruskal-Wallis test) among the treatments, with the communities under high nutrients taking approximately 6 days to regenerate and the communities under low nutrients taking > 18 days.

Resilience was much slower for AFDM than for chlorophyll *a* under high nutrients and did not re-develop at all under low nutrients (Fig. 8.2a,b). By Day 23 AFDM was still well below pre-disturbance levels in the high nutrient treatments, but was accruing at a rate similar to Day 8 - 15 communities (data not shown, but see Fig. 8.2 a,b).

**TABLE 8.7** F-ratios from an analysis of variance of the effects of the disturbance (comparison of the pre-disturbance Day 15 communities with those after the disturbance on Day 18), light intensity and nutrients (two levels for each parameter) on the most common periphyton taxa (* = $P$ <0.05, ** = $P$ <0.01, *** = $P$ <0.001).

| | ANOVA F-values | | | | |
|---|---|---|---|---|---|
| Source | *Achnanthidium* | *Fragilaria* | *Schizothrix* | *Gomphonema* | *Navicula* |
| Disturbance (D) | 1.5 | 3.7 | 0.0 | 2.4 | 0.0 |
| Light (L) | 0.9 | 0.2 | 13.0*** | 0.4 | 1.4 |
| Nutrients (N) | 98.2*** | 20.6*** | 2.7 | 1.4 | 0.1 |
| D x L | 1.1 | 3.9 | 0.1 | 2.3 | 0.3 |
| D x N | 0.1 | 4.7* | 0.1 | 1.5 | 1.8 |
| L x N | 2.5 | 0.2 | 2.7 | 1.6 | 0.5 |
| D x L x N | 2.3 | 4.2 | 0.0 | 0.8 | 2.9 |

*Overall impacts of the disturbance on accrual dynamics and successional trajectories*

Maintaining an undisturbed control community for each resource treatment enabled me to assess how important such physical disturbances are to longer term biomass dynamics and successional trajectories of the periphyton. Major differences were found in the degree that disturbance re-set biomass variables among the resource treatments. Disturbance intially re-set chlorophyll *a* concentrations by three days in the HL, HN treatment compared with its undisturbed equivalent, but AFDM accrual was reset by eight days (Table 8.4). Disturbance of the LL, HN treatment re-set AFDM development by three days, but chlorophyll *a* by eight days. The discrepancy between these variables in the two treatments (and compared with the resistance results) I attribute to the HL, HN community having a higher growth rate than its low light equivalent at the time of the disturbance, so that the re-set impact on chlorophyll *a* was less. Further, the impact of the disturbance on the HL, HN AFDM was greater than the low light equivalent because, although AFDM accrual rates were similar in the two treatments, the high light community had a much lower bulk density and thus was more vulnerable. Disturbance set AFDM and chlorophyll *a* concentrations in the low nutrient treatments back by 14 - 16 days, almost to the beginning of the accrual cycle.

The disturbance also reduced community growth rates relative to undisturbed communities (Table 8.3). However, the reduction varied considerably depending on the resource treatment. The smallest reduction occurred in the most resistant LL, HN community. Growth rate was reduced by 40% in the HL, HN community; by 82% in the HL, LN community; and by 90% in the LL, LN community. These differences were only statistically significant (i.e., $p < 0.05$) for the LL, LN treatment because the small number of samplings for determination of rates limited the statistical power, but did suggest a coupling between resistance and resilience in these communities.

There were long-term consequences of these large disturbance mediated reductions in growth rates for the three least resistant communities (i.e., HL, HN; HL, LN; and LL, LN). Disturbance resulted in biomass development falling progressively further behind in the disturbed treatment than the undisturbed control. For example, the initial reset of three days increased to nine days by the end of the experiment for the HL, HN community. Because growth rates were so severely reduced in the low nutrient treatments, biomass in the post-disturbance phase largely reflected what had survived the disturbance (i.e., biomass reflected the degree of resistance) (Fig. 8.2 a,b). However, because growth rates were reduced by much less in the high nutrient treatments, regrowth in these communities contributed a much greater (and

increasing) proportion of the biomass in the post-disturbance phase (i.e., biomass reflected the degree of resilience).

The loss of biomass as a result of the disturbance, and the reduction in post-disturbance growth rates, resulted in major overall differences in average biomass between the control and disturbed communities over the 27 day duration of the experiment (Table 8.8). Average chlorophyll *a* concentration was reduced more than average AFDM by the disturbance. Further, these differences were smaller under the low nutrient treatment suggesting that the disturbance had a lower long-term relative impact on these communities. Disturbance reduced the concentrations of chlorophyll *a* by approximately 50% in the two high nutrient treatments. The HL, LN treatment was reduced by 38% and the LL, LN community was not reduced at all.

My data on relative abundance of taxa was condensed into principal component factors in species space to quantitatively evaluate the effects of the disturbance on overall successional trajectories. The first two principal factors explained 29 % and 23 % of the variance in relative abundance of the taxa. Factor 1 mainly carried information about the relative abundance of *Achnanthidium* ($r$ = -0.893 for the correlation between the relative abundance of *Achnanthidium* and Factor 1 scores), centric diatoms ($r$ = 0.782), and *Fragilaria* ($r$ = 0.748). Factor 2 was most strongly weighted by the relative abundances of *Nitzschia* ($r$ = 0.846) and *Schizothrix* ($r$ = 0.679).

Two distinct trajectories, which differ as a function of nutrient treatment, are evident (Fig. 8.5). For the nutrient enriched treatment the communities had a simple unidirectional successional trajectory that reflected a decrease in the relative abundance of *Achnanthidium* and an increase in *Fragilaria* (Factor 1), together with an increase in the relative abundance of centric diatoms, *Schizothrix* and *Nitzschia* (Factor 2) from Day 15 to Day 27. The disturbance resulted in moderate displacement of the direction of species succession in the high nutrient treatments (Fig. 8.5). However, by Day 27 in both high-nutrient light treatments the succession had started to loop back toward the undisturbed communities, proceeding along the same developmental trajectory. Unity with the undisturbed communities did not occur within the duration of the experiment. Thus, the disturbance had set the course of community succession back at least 9 days. For the low-light, high-nutrient communities (which lost the least amount of chlorophyll *a* with the disturbance, Table 8.4), there was only a small displacement in community structure (mainly along the

**TABLE 8.8** Summary of mean AFDM and chlorophyll *a* over the accrual cycle (Days 0, 8, 15, 18, 20, 23, 27) for control and disturbed communities as a function of resource treatment (1, paired T-test of control vs disturbed; * , $P < 0.05$; **, $P < 0.010$)

| | | AFDM ($g.m^{-2}$) | | | Chlorophyll *a* ($mg.m^{-2}$) | | |
|---|---|---|---|---|---|---|---|
| Resource treatment | | Control | Disturbed | T-statistic[1] | Control | Disturbed | T-statistic[1] |
| High light, high nutrients | $\bar{x}$ | 14.2 | 4.8 | 2.684* | 94.5 | 42.6 | 3.650** |
| | S.E. | 5.2 | 1.4 | | 31.4 | 15.6 | |
| High light, low nutrients | $\bar{x}$ | 2.8 | 1.7 | 1.287 | 2.6 | 1.6 | 0.725 |
| | S.E. | 0.7 | 0.7 | | 1.2 | 1.2 | |
| Low light, high nutrients | $\bar{x}$ | 12.7 | 5.5 | 2.959* | 78.5 | 40.7 | 4.044** |
| | S.E. | 4.5 | 1.4 | | 24.8 | 12.3 | |
| Low light, low nutrients | $\bar{x}$ | 3.5 | 1.5 | -0.588 | 1.2 | 1.2 | 0.566 |
| | S.E. | 0.9 | 0.6 | | 0.4 | 0.8 | |

Factor 2 axis with a reduction in *Nitzschia* sp. and *Schizothrix* sp.). The disturbed communities had almost merged in structure with the Day 20 undisturbed communities by Day 27 (9 days after the disturbance). Thus, the disturbance had set back community development in this treatment by only 7 days.

However, for the low nutrient treatment there was no directional successional sequence (Fig. 8.5). The principal components initially had a greater weighting on Factor 1 with most of the movement for Days 20 and 23 along this axis for both the undisturbed and disturbed communities. However, by Day 27 the communities were starting to have a greater weighting on Factor 2 taxa (*Nitzschia* and *Schizothrix*). The disturbance only caused a minor displacement of this taxonomic trajectory for the HL, LN community and subsequent shifts in structure of the disturbed community mirrored the undisturbed control community. Although this trend also occurred in the LL, LN community, there was a greater initial displacement associated with the disturbance.

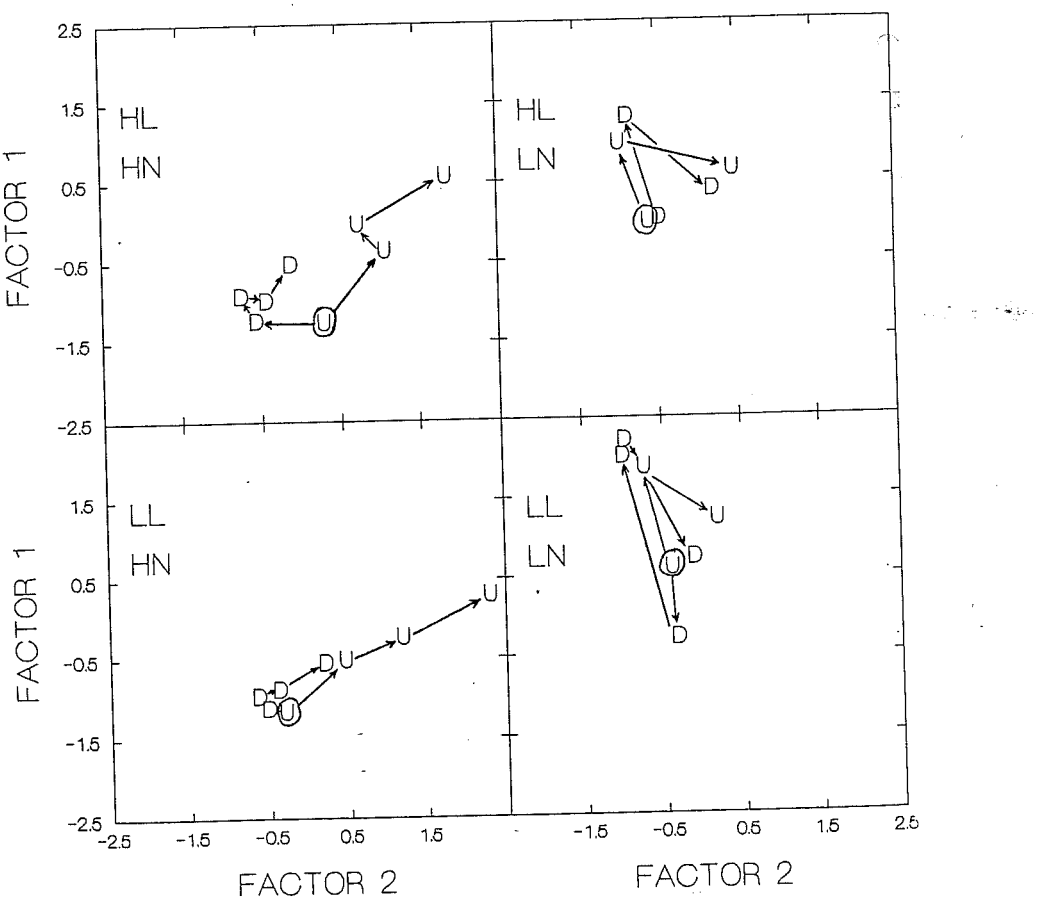


Fig. 8.5: Growth trajectories as described by the first two factors of the communities' principal components for the undisturbed (U) vs. disturbed (D) communities (see Fig. 8.3 for a definition of resource treatment abbreviations in the top left of each panel).

## IV. Discussion

In this study I found that disturbance and resource availability interacted to control periphyton community dynamics. Variations in resource supply had important effects on both disturbance resistance and resilience. The variations in resistance were mediated through physiological rather than taxonomic differences. Overall, the most disturbance resistant communities developed under conditions of low light, but high nutrient supply. The most resilient communities developed under conditions of both high light and high nutrients. Average biomass of the high nutrient treatments was more strongly influenced by resilience than by resistance. Under low resource supply the communities displayed both weak resistance and weak resilience, with resistance being the dominant determinant of average biomass. These results largely support my initial hypotheses that: a) under conditions of low light and low nutrient resources, periphyton communities would have low resilience to disturbance with average biomass during the recovery phase primarily reflecting community resistance (i.e., percentage of biomass remaining after disturbance); and b) under high light and high nutrients community resistance would also be low, but post-disturbance resilience would be high and average biomass during the recovery phase would primarily reflect this resilience.

A quantitative evaluation of the average biomass component of Fig. 8.1, and associated hypotheses, is possible by placing quantitative parameter ranges on the axes. This can be done using growth rate ($r$) as a measure of resilience (setting the scale to reflect the full range of values from severely nutrient limited to nutrient saturated growth; after Biggs 1990), and using the percentage loss of chlorophyll *a* as a measure of resistance (since only one disturbance was measured). I can also parametize the diagonal low to high biomass gradient on Fig. 8.1 with values of 0 - $\geq$100 mg/m$^2$ chlorophyll *a* (since proliferation conditions are considered to occur at > 100 mg/m$^2$ chlorophyll *a*; Horner et al. 1983). The location of the undisturbed and disturbed resource treatments as functions of $r$ and chlorophyll *a* loss is given in Fig. 8.6, together with the measured mean accrual cycle chlorophyll *a*. There was reasonable agreement between these measured values and those predicted from the conceptual model defined in Fig. 6.2 (Chapter 6) in six out of eight comparisons (Table 8.9). Poor agreement was found for the undisturbed, unenriched communities. This appeared to have been a consequence of only moderate growth rates of the initial thin-film communities, and their inability to sustain biomass at low nutrient levels. Therefore, autogenic sloughing soon set in, and long-term biomass became quite low.

Overall, observed biomass values agreed reasonably well with predicted values and supported the conceptual model (Fig. 8.1).

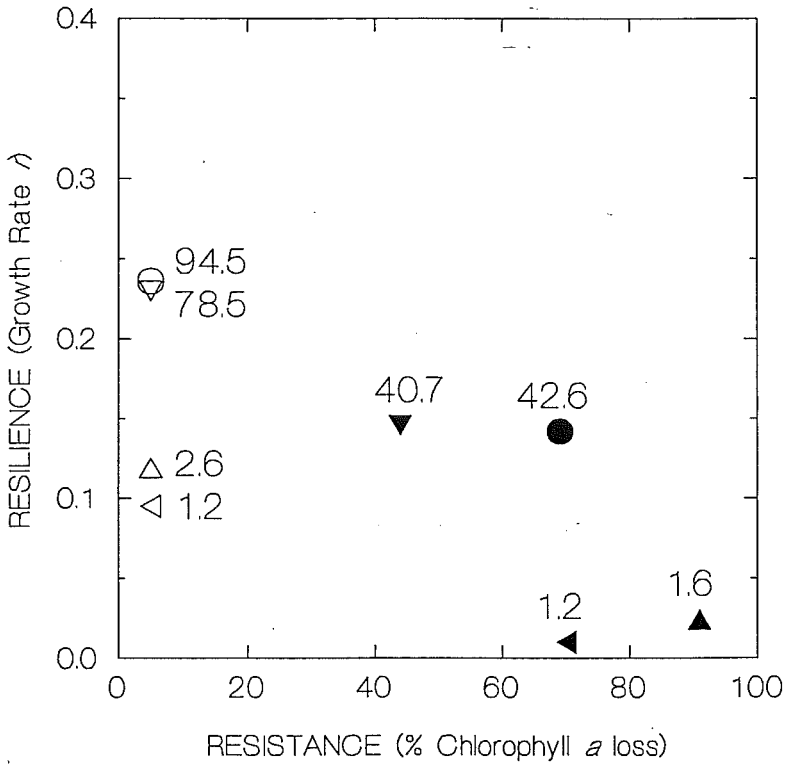


Fig. 8.6: Growth rate (resilience) plotted against percentage chlorophyll a loss (resistance) for the experimental treatments. The points adjacent to the y-axis should be at zero % chlorophyll loss, but have been offset to clarify the plot. Mean accrual cycle chlorophyll *a* is given for each treatment. O = HL,HN; △ = HL, LN; ▽ = LL, HN; ◁ = LL, LN. Open symbols = control, filled = disturbed treatments.

*Effects of nutrients and light on periphyton community structure and function*

Community development was more strongly limited by nutrients than by light. The addition of N and P stimulated growth rates (*r*), peak biomass, relative abundance of *Achnanthidium minutissimum*, areal and chlorophyll-specific community metabolism, % chlorophyll *a*, % C, % N, and bulk density. The peak biomass observed in the enriched communities after 23 days accrual (approximately 180 mg $m^{-2}$ chlorophyll *a*) was very similar to that recorded elsewhere for P saturated growth in diatom communities over a similar time period (Bothwell 1989). However, the maximum growth rates (*r*) were only half those expected for phosphorus saturated growth kinetics in epilithic diatoms (Biggs 1990). Unexpectedly, a major change in taxonomic structure did not occur as a function of the different resource regimes (see below).

**TABLE 8.9** Observed vs predicted mean accrual cycle chlorophyll *a* for the undisturbed and disturbed communities as a function of resource treatment. See text for derivation of predicted chlorophyll *a*.

| | Treatment | Predicted chlorophyll *a* ($mg.m^{-2}$) | Observed chlorophyll *a* ($mg.m^{-2}$) |
|---|---|---|---|
| 1 | **Undisturbed** | | |
| | High light, high nutrients | 70-80 | 94.5 |
| | High light, low nutrients | 50-60 | 2.6 |
| | Low light, high nutrients | 70-80 | 78.5 |
| | Low light, low nutrients | 50-60 | 1.2 |
| 2 | **Disturbed** | | |
| | High light, high nutrients | 40-50 | 42.6 |
| | High light, low nutrients | <5 | 1.6 |
| | Low light, high nutrients | 30-40 | 40.7 |
| | Low light, low nutrients | <5 | 1.2 |

The much higher bulk density of the enriched communities, and also the effect of light on this, was unexpected. In the high nutrient treatments the cells appeared to be more densely packed (probably because of faster accrual in the higher resource environments and thus a lower impact of density-dependent resource competition; Stevenson et al. 1991). I expected to see a response to light and nutrients like that reported by Lowe et al. (1986). They found that communities growing in shaded conditions were composed of erect taxa (predominantly diatoms), whilst in higher light conditions and more enriched environments, they were more diverse in physiognomy and forming a thicker mat dominated by filamentous taxa. Mulholland et al. (1991) have reported similar physiognomic responses to high nutrient supply in laboratory streams. The low physical diversity of my artificial streams, and the relatively high velocities, could have contributed to the lack of any major differences in taxonomic response to nutrient additions.

It is difficult to explain why the high light communities were comparatively loosely aggregated (i.e., had a low bulk density). One possibility is that more mucilage production is occurring as an acclimation strategy to high light intensities (photoinhibition has been recorded for periphyton communities not acclimated to high light at intensities of 1100 $\mu mol/m^2/s$, Boston and Hill 1991). I anticipate that such mucilage material would have a much lower bulk density and be more prone to physical abrasion than the adnate/prostrate cells of the LL, HN treatment.

Light manipulation had a lower-order effect on community composition than nutrients. Light on its own only affected the relative abundance of the filamentous cyanobacterium *Schizothrix*, which was significantly greater under low light, and on mat bulk density. However, a strong interaction between light and nutrients affected several of the community variables. The most pronounced was the affect on % chlorophyll *a* which was significantly higher in the high nutrient treatments, particularly in combination with low light. While shade adapted cells can contain 2 - 10 times more chlorophyll than high-light cells (Darley 1982), the higher % chlorophyll *a* in the HL, HN treatment (cf. HL, LN treatment) suggests that chlorophyll *a* production was nutrient limited; implying that the communities could not chromatically adapt to low light under low nutrient conditions.

The addition of nutrients also strongly affected the biomass dynamics of the communities. Under low (ambient) nutrient concentrations, peak biomass was recorded after only 15 days of accrual (8 days sooner than under the high nutrient treatment). By Day 20 these communities had commenced sloughing, with peak biomass under high light conditions being 3 times higher than under low light (9 vs. 3 mg $m^{-2}$ chlorophyll *a*). Thus, resource limitation altered the abundance (light and nutrients) and the dynamics (nutrients) of these communities. This limitation was probably due to lower rates of nutrient mass transfer (Stevenson and Glover 1993) and lower light flux (Jorgensen and Des Marais 1988, Dodds 1992) to the base of the community resulting in earlier die-back of the basal cells. These results are consistent with those of Lohman et al. (1992) who reported that peak chlorophyll *a* was reached sooner (with lower absolute concentrations), in unenriched than enriched streams in the Ozark Mountains, U.S.A. In contrast, communities in the enriched streams continued to grow rapidly in biomass through to Day 23 with a peak in chlorophyll *a* which was approximately the same for both light treatments. However, the peak was 20 times higher for the HL, HN treatment and 60 fold higher for the LL, HN treatment compared with their respective low nutrient counterparts. Thus, the communities were being regulated by both nutrients and light, with nutrients being most resource limiting. These findings are similar to those of Bothwell (1988) who reported that seasonal light effects on periphytic diatom growth rates only occurred in his diatom communities if nutrients were replete. Conversely, Hill and Knight (1988) found that nutrients stimulated periphyton in an unshaded Californian stream, but not in a shaded stream suggesting that shading had an overriding effect at their site. The reason for the discrepency between my results and those of Hill and Knight is possibly that my low-light levels were still quite high (200 - 400 $u$E/$m^2$/s). By Day 27, sloughing had commenced in both the high nutrient treatments, but was

significantly greater under low light. The importance of both nutrient and light availability to community dynamics is re-inforced by these findings. They also suggest that under nutrient replete conditions light may become an important regulator of autogenic sloughing and, possibly, carrying capacity.

*Resistance as a function of resource regimes.*

The disturbance-mediated loss of biomass varied greatly as a function of the different light and nutrient treatments. Thus, differential resource supply to the periphyton confered different degrees of resistance to disturbance. The communities were all dominated by *Achnanthidium* (78 - 93% of live cells) suggesting that the differential resistance was mainly determined by community physiology rather than taxonomic composition. The LL, HN community had the highest resistance to disturbance as measured by the percentage loss of both AFDM and chlorophyll *a*. A number of factors may have contributed to its high resistance. It had the highest pre-disturbance GPP, % chlorophyll *a*, % carbon, % nitrogen, and mat bulk density, and the lowest C:N ratio. In contrast, the more nutrient stressed HL, LN community had the least resistance. The communities growing under the lowest resource supply treatment (low nutrient, low light) appeared to be in a very physiologically stressed condition (Table 8.1) and had commenced a phase of natural degradation which may have compounded this effect. Conversely, Mulholland et al. (1991) found that nutrient input alone had little effect on resistance. However, their high SRP concentrations were similar to my low nutrient treatment so their communities may have been somewhat nutrient stressed. In other studies, variable resistance has been attributed to both inherent (physical attributes of the dominant taxa) and conditional (environmental factors affecting community strength and community age) properties of the communities (see Chapter 3). Thus, the different physiological responses of periphyton communities represent yet another factor potentially affecting resistance properties.

The LL, HN treatment resulted in a community with considerable disturbance resistance. It had high bulk density, was thin, and very condensed. It also lacked an overstory canopy and was therefore less susceptible to shear stress forces. Mulholland et al. (1991) found that physical stress by snail grazing also increased resistance by removing loosely adhering taxa and confering dominance to low-profile, tightly adhering species, that have high inherent resistance to shear stress (see Chapter 3). Similarly, Peterson and Stevenson (1992) have shown that physical stress brought about by high water velocities can also enhance periphyton disturbance resistance. Thus, a number of stresses can confer increased disturbance resistance on

periphyton. Further, my results suggest that moderate to low levels of (resource) stress are most beneficial to resistance, but high stress can decrease resistance (cf. Steinman and McIntire 1990).

As has been reported for natural rivers (Biggs and Close 1989), and experimental streams (Peterson and Stevenson 1992), AFDM (a composite of living and decaying/dead organic matter) was more susceptible to removal by the disturbance than the actively growing biomass (as represented by chlorophyll *a*). Although much of the difference in percentage removal of these two parameters appeared to be due to loss of detritus, the associated heterotroph loss must also have been significant since community respiration was reduced by the disturbance, but GPP was not. Also, % C and % N increased as a result of the disturbance, particularly in the enriched treatments.

The removal of detritus and associated heterotrophs by the disturbance (which in-turn reduced CR and enhanced % C and % N) and an increase in the relative abundance of diatoms, is perhaps analogous to the effect of disturbance of terrestrial vegetation by fire. Both natural and anthropogenic burning removes accumulations of organic debris and re-mineralizes nutrients, frees herbaceous species from competition, maintains the more nutritious (high protein) growing tips down in the herbivore browse zone, and re-invigorates fire resistant canopy species (Daubenmire 1974). Such events can have a stimulatory effect on subsequent growth and dominance of survivors and can improve the food quality of vegetation for herbivores. My results strongly suggest that similar effects occur in streams with moderate intensity flood disturbances. In particular, I found that disturbance increased cellular N concentrations by up to 88% and decreased C:N ratios by up to 29%. Similarly, Humphrey and Stevenson (1992) reported an increase in cellular N following elevated velocities in an enriched periphyton community, but in contrast to my results found that the simulated disturbance decreased N in unenriched communities. The enhancement of nitrogen concentrations and the reduction in C:N ratios by biomass-scouring disturbances has potentially important ramifications for higher trophic levels in streams and to stream energetics.

*Resilience as a function of resource regimes*

Communities in the high nutrient treatments were more resilient following disturbance than those in the low nutrient treatments. Indeed, the communities growing under low nutrient conditions never really recovered from the disturbance. Because of the very low rate of immigration from the stream populations in my

experiment (as evidenced by low initial accrual trajectories), re-development in the enriched troughs probably resulted primarily from in-situ growth, rather than from immigration. Steinman et al. (1991) and Mulholland et al. (1991) also reported nutrient enhancement of resilience (as measured by *r*) for light elimination and scour disturbances in laboratory streams. Grimm and Fisher (1986) have also emphasised the importance of nutrients for recovery of Sonoran desert streams from disturbance.

The reduction in growth rates following the disturbance was unexpected since disturbing the communities removed algal overstory biomass and detritus. I expected detritus in the undisturbed community to have reduced competition for light and nutrient availability through bacterial sequestering. Such negative effects of shear stress disturbance on periphyton growth rates have been reported previously by Humphrey and Stevenson (1992) in low nutrient, but not high nutrient environments. These responses may be related to the effects of currents stressing cell membranes which in-turn could promote cell nutrient leakage and the loss of nutrient harvesting exoenzymes (Borchardt et al. 1994).

The disturbance in the high nutrient treatments initially set chlorophyll *a* concentrations back to those found in the communities 3 days before. However, as noted above, the communities did not resume the same trajectory of accumulation as in the undisturbed communities. Thus, by the end of the experiment the disturbance had set the biomass development back by 9 days. Interestingly, the taxonomic composition of the most resistant LL, HN communities (where a 44 % loss of chlorophyll *a* occurred) returned to that of a Day 20 undisturbed community, only seven days after the disturbance showing that the taxonomic development of this community was less severely affected than biomass. The taxonomic development of the more disturbed HL, HN treatment communities (69 % loss of chlorophyll *a*) was more severely affected, however. Nine days after the simulated disturbance it still had not re-attained the composition of the undisturbed communities.

My results suggest that resistance and resilience are positively coupled and that they are not inversely related as suggested by Webster et al. (1975). I would expect that the more biomass left behind after a disturbance, the greater the resilience because propagule re-colonization is not required. However, such a scenario is complicated somewhat under resource stress. For example, while resilience and resistance were low in both low light communities, the post-disturbance growth rate of the high light (low nutrient) community was almost twice that of the low light (low nutrient) community.

*Implications for stream ecology*

Light and nutrient supply varies widely among streams flowing through forest, scrub, prairie and agricultural lands. My results suggest that such differences in resource regimes could have a major influence on the way the periphyton responds to a given flood. They suggest that under low and high limiting resources, resistance to disturbance tends to be low, but with low resources resilience also tends to be slow resulting in low long-term average biomass. Conversely, a small degree of resource stress (e.g., light stress through shading in an enriched stream) may enhance the resistance of the periphyton without compromising resilience. As could be expected, disturbance had the least long-term impact on the highly nutrient limited communities because biomass accrual was already low. I further conclude that disturbance and resource stress are not operating independently to govern the overall state of periphyton development in stream ecosystems. Disturbances that only partially remove biomass may have an important effect on higher trophic levels by removing accumulated detritus and improving food quality for herbivores.

## V. Summary

This chapter describes an experiment designed to investigate in more detail the interactions between disturbance and resource supply for stream periphyton. In particular the effects of differences in light and nutrients (emulating conditions in shaded-unshaded and enriched-unenriched streams) on resistance and resilience processes were examined. The experiment was carried out in outdoor experimental troughs. Light treatments were applied to half the lengths of all troughs using neutral density filters and four of the troughs had nutrients added continuously from a reservoir. A uniform (simulated) scouring disturbance was applied to all troughs during the exponential growth phase of the periphyton. A set of substrate tiles was removed from each resource treatment just prior to the disturbance and replaced immediately following it to act as a control against which the effects of the disturbance could be measured. Resistance was determined as the percentage biomass loss over the period of the disturbance, and resilience as the relative rates of regrowth and relative time to return to pre-disturbance biomass.

Low nutrients were found to be more limiting to growth than the low light treatment, and resistance to a simulated disturbance varied significantly as a function of resource supply. Loss of chlorophyll *a* due to the disturbance ranged from 44% under the low light, high nutrient treatment, to 91% under the high light, low nutrient treatment.

Resistance was affected by both nutrients and light supply, and was mediated through differences in community physiology but not differences in taxonomic composition. The disturbance reset chlorophyll *a* concentrations of communities provided with a high nutrient supply to levels observed 3 - 8 days earlier, but low nutrient supply communities took about 16 days to re-establish to pre-disturbance levels. Overall, the applied disturbance affected taxonomic composition, reduced respiration and enhanced % chlorophyll a, % carbon, and % nitrogen of the periphyton mat. Resilience also varied significantly as a function of resource supply, and was highest for the high nutrient treatments. The disturbance reduced growth rates in three of the resource treatments and altered successional trajectories in the enriched treatments, but not the unenriched ones. As with resistance, resilience was greatest for communities grown under higher resource supply. The average biomass of the treatments was well predicted by the disturbance - resource stress - grazer model.

## VI. References

Biggs, B. J. F. 1990. Use of relative specific growth rates of periphytic diatoms to assess enrichment of a stream. *N.Z. J. Mar. Freshw. Res.* 24:9-18.

Biggs, B. J. F. & Close, M. E. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biol.* 22:209-31.

Borchardt, M. A., Hoffmann, J. P. & Cook, P. W. 1994. Phosphorus uptake kinetics of *Spirogyra fluviatilis* (Charophyceae) in flowing water. *J. Phycol.* 30:403-17.

Boston, H. L. & Hill, W. R. 1991. Photosynthesis-light relations of stream periphyton communities. *Limnol. Oceanogr.* 36:644-56.

Bothwell, M. L. 1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. *Can. J. Fish. Aquat. Sci.* 45:261-70.

Bothwell, M. L. 1989. Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Can. J. Fish. Aquat. Sci.* 46:1293-301.

Darley, W. M. 1982. *Algal Biology: a physiological approach.* Blackwell Scientific, Oxford, .

Daubenmire, R. F. 1974. *Plants and Environment: A textbook of autecology.* John Wiley & Sons, New York, .

DeAngelis, D. L., Mulholland, P. J., Elwood, J. W., Palumbo, A. V. & Steinman, A. D. 1990. Biogeochemical cycling constraints on stream ecosystem recovery. *Environmental Management* 14:685-97.

DeNicola, D. M., Hoagland, K. D. & Roemer, S. C. 1992. Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *J. North Am. Benthol. Soc.* 11:391-404.

Dodds, W. K. 1992. A modified fiber-optic light microprobe to measure spherically integrated photosynthetic photon flux density: Characterization of periphyton photosynthesis-irradiance patterns. *Limnol. Oceanogr.* 37:871-78.

Fisher, S. G. & Grimm, N. B. 1988. Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verh. Internat. Verein. Limnol.* 23:1183-90.

Grimm, N. B. & Fisher, S. G. 1986. Nitrogen limitation in a Sonoran Desert stream. *J. North Am. Benthol. Soc.* 5:2-15.

Grimm, N. B. & Fisher, S. G. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *J. North Am. Benthol. Soc.* 8:292-307.

Hickey, C. W. 1988. Benthic chamber for use in rivers: testing against oxygen mass balances. *Journal of Environmental Engineering* 114:828-45.

Hill, W. R. & Knight, A. W. 1988. Nutrient and light limitation of algae in two northern California streams. *J. Phycol.* 24:125-32.

Horner, R. R., Welch, E. B. & Veenstra, R. B. 1983. Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. *In* R.G. Wetzel *Periphyton of Freshwater Ecosystems.* Junk, The Hague, pp. 121-34.

Humphrey, K. P. & Stevenson, R. J. 1992. Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates. *J. North Am. Benthol. Soc.* 11:37-48.

Jorgensen, B. B. & Des Marais, D. S. 1988. Optical properties of benthic photosynthetic communities: Fiber-optic studies of cyanobacterial mats. *Limnol. Oceanogr.* 31:99-113.

Lohman, K., Jones, J. R. & Perkins, B. D. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. *Can. J. Fish. Aquat. Sci.* 49:1198-205.

Lowe, R. L., Golladay, S. W. & Webster, J. R. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *J. North Am. Benthol. Soc.* 5:221-29.

Luttenton, M. R. & Rada, R. G. 1986. Effects of disturbance on epiphytic community architecture. *J. Phycol.* 22:320-26.

Mulholland, P. J., Steinman, A. D., Palumbo, A. V. & DeAngelis, D. L. 1991. Influence of nutrients and grazing on the response of stream periphyton communities to a scour disturbance. *J. North Am. Benthol. Soc.* 10:127-42.

Peterson, E. G. & Stevenson, R. J. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73:1445-61.

Power, M. E. & Stewart, A. J. 1987. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 117:333-45.

Robinson, C. T. & Rushforth, S. R. 1987. Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiol.* 154:49-59.

Sartory, D. P. & Grobelaar, J. E. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiol.* 114:177-87.

Steinman, A. D. & McIntire, C. D. 1990. Recovery of lotic periphyton communities after disturbance. *Environmental Management* 14:589-604.

Steinman, A. D., Mulholland, P. J. & Kirschtel, D. B. 1991. Interactive effects of nutrient reduction and herbivory on biomass, taxonomic structure and P uptake in lotic periphyton communities. *Can. J. Fish. Aquat. Sci.* 48:1951-59.

Steinman, A. D., Mulholland, P. J., Palumbo, A. V., Flum, T. F., Elwood, J. W. & DeAngelis, D. L. 1990. Resistance of lotic ecosystems to a light elimination disturbance: a laboratory stream study. *Oikos* 58:80-90.

Stevenson, R. J. & Glover, R. 1993. Effects of algal density and current on ion transport through periphyton communities. *Limnol. Oceanogr.* 38:1276-81.

Stevenson, R. J., Peterson, C. G., Kirschtel, D. B., King, C. C. & Tuchman, N. C. 1991. Density-dependent growth, ecological strategies and effects of nutrients and shading on benthic diatom succession in streams. *J. Phycol.* 27:59-69.

Webster, J. R., Waide, J. B. & Patten, B. C. 1975. Nutrient recycling and stability of stream ecosystems. *In* F.G. Howell, J.B. Gentry & M.H. Smith *Mineral cycling in southeastern ecosystems.* United States Energy Research and Development Administration, Washington, DC, pp. 1-27.

Wilkinson, L. 1990. *SYSTAT: The system for statistics.* SYSTAT Inc, Evanston IL, .

# Chapter 9

## Summary and General Conclusions

Studies involving stream periphyton have blossomed in the last five - ten years. The community is now widely recognised as a fundamental source of energy to streams and has the potential to form extensive proliferations. Much of this recent research, however, has focussed on small scale processes (e.g., grazing), many of which only operate in relatively benign hydrological environments. To develop our understanding of why periphyton communities in streams of one region may be different from those in another requires field based studies of many systems over broad environmental gradients (e.g., Biggs et al. 1990).

The detailed pioneering work on single streams by Douglas (1958), Tett et al. (1978) and Fisher et al. (1982), together with the multiple stream comparisons of Biggs (1988), Fisher & Grimm (1988) and Biggs & Close (1989) have all shown how important hydraulic disturbance can be in controlling periphyton development in temperate and desert region streams. Since these studies were undertaken there has been further extensive single stream and experimental research that has greatly enhanced our knowledge of disturbance responses at the population and community level (e.g., Grimm & Fisher 1989, Peterson & Stevenson 1990, DeAngelis et al. 1990, Steinman et al. 1990, Stevenson 1990, Mulholland et al. 1991, Peterson and Stevenson 1992, Peterson & Grimm 1992, Boulton et al. 1993, Peterson et al. 1994). The contribution of the research described in this thesis is that it quantifies the actual physical attributes of hydraulic disturbance and the kinetics of loss processes so that, for the first time, biotic responses can be assessed against known disturbance intensities and frequencies. Thus, I was able to make comparisons across broad geographic regions based on streamflow records and knowledge of channel hydraulic geometry.

Utilising this approach, it was possible in Chapter 2 to demonstrate the overiding importance of differing disturbance frequencies in controlling average periphyton biomass among a set of 16 New Zealand streams. Resource supply was important, but only if there was a sufficiently low frequency of disturbance events to allow these resources to be utilised and translated into accrued biomass.

The experimental studies described in Chapter 3 focussed on the shear stress - loss processes occurring with the onset of a flood to obtain a greater understanding of the actual forces required to dislodge different community types (i.e., in ecological terms a definition of variable community "resistance"). My results demonstrated that disturbance is very much an interactive process involving forces applied and the

ability of the community to resist the drag created. Thus, the response of different communities to a given level of shear stress was found to be highly variable. For example, the loss of the filamentous periphyton was not a simple linear function of increases in shear stress with the onset of a disturbance, such that relatively large amounts would be dislodged from the stream bed with small increases in flow forces. Nevertheless, the loss rate of adnate diatoms was a linear function of increased shear stress. The work described in Chapter 3 clearly showed that a given incremental increase in flow in one catchment may represent a significant disturbance for periphyton, but the same proportional flow change may not be a disturbance in another catchment. In particular it indicated that in enriched streams (where filamentous taxa tend to dominate) high flow events with only a relatively low magnitude of change in forces may cause major disturbance of periphyton. A further significant finding was that even at the highest shear stresses likely to be found in most streams during floods (90 N $m^{-2}$) significant fractions of diatom communities (~ 50%) remained on the substrata. This indicates that in unenriched streams, where such communities tend to dominate, very large changes in flow, accompanied by physical abrasion by moving bed sediments, will be required for major flood disturbance of communities to occur. This experimental work corroborated the field based results reported in Chapter 2 where strong disturbance control of average biomass was demonstrated in enriched and moderately enriched streams, but not in unenriched streams.

In Chapters 4 and 5 I used further field based studies to focus on the recovery (i.e., "resilience") and spatial distribution of climax communities as functions of post-flood hydraulic conditions. Recovery was initially fastest in areas of low water velocity, but was overtaken later during the exponential growth phase of the accrual cycle by those communities growing in places of high water velocity (with intermediate velocity areas growing at an intermediate rate). Low velocity communities reached peak biomass first and began sloughing first (presumably through mass transfer limitation), followed by high velocity communities which exhibited drag limitation. Sloughing of intermediate velocity communities did not occur within the 92 day sampling period of the study. At maturity, peak biomass occurred at velocities of 0.5 - 0.7 m $s^{-1}$. In the second recovery study (Chapter 5), I re-analysed (in considerably more detail) the relationship between peak biomass and spatial variations in hydraulic conditions. Unexpectedly, no clear unimodal hydraulic habitat preferences were demonstrated by dominant diatom taxa, AFDM biomass continued to increase with near-bed velocities up to 1.5 m $s^{-1}$, chlorophyll *a* concentration and gross primary production did not change significantly across the

velocity gradient, but community respiration increased with velocity. These findings demonstrate the complexity of responses that stream periphyton communities have to hydraulic disturbance and stress. They indicate the need to take into account community type when assessing not only disturbance resistance, but also disturbance resilience.

The understanding obtained from the preceeding studies (particularly Chapter 2), together with that from the literature, were brought together in the form of a conceptual model for stream periphyton in Chapter 6. I hypothesised that different periphyton taxa have evolved to exploit specific niches defined by different disturbance frequencies (through differential abilities to resist shear stress perturbations and exploit inter-disturbance windows of hydraulic stability), and the interaction of these traits with resource capture abilities and susceptibility to invertebrate grazing (controlled by production vs. consumption). Four main guilds of taxa were identified that exploit different portions of the habitat matrix and form high biomass in the area of low disturbance frequency, and high limiting resource supply, but low biomass in the area of high disturbance frequency no matter what the level of resource supply. Furthermore, grazers were proposed to have significant impact on periphyton biomass in habitats where flood disturbance is moderate to low and resource supply is also moderate to low.

The habitat model was tested using both field and experimental studies in Chapters 7 and 8. In the first of these studies, periphyton biomass and community structure were monitored at three sites (incorporating both riffles and runs) for nearly 2 years along a foothills river, together with hydraulic disturbance parameters and the nutrient resource regime. Major differences in community structure and biomass occurred in the riffles along the river and a longitudinal gradient of increasing nutrient enrichment appeared to be controlling this rather than major differences in disturbance regimes. In contrast, run communities showed no response to this nutrient gradient apparently because of intense invertebrate grazing that reduced algal biomass by an estimated 60% or more. The model predicted both biomass and composition of communities growing in riffles (but not runs) reasonably well.

In the second study (Chapter 8), light and nutrient resource conditions were manipulated to put growing periphyton under varying degrees of resource stress and their response (in terms of resistance and resilience) to a moderate intensity flood (elevated velocities and gravel abrasion) was determined. Few invertebrate grazers were present. The varying resource treatments caused major differences in the way

the communities responded and were mediated through differences in community physiology rather than differences in taxonomic composition. The most resistant community was that grown under some physiological stress (low light, but high nutrients). The more stressed, low nutrient communities were heavily impacted by the disturbance, and post-disturbance resilience was considerably faster in the high nutrient treatments. Nevertheless, the disturbance reduced growth rates in these latter communities and altered their successional trajectories.

The original goal of my research was to more clearly define the role of hydraulic disturbance in determining the development of periphyton in stream ecosystems, and to provide a physical basis by which disturbance intensity and frequency could be defined. I believe that this goal has been achieved. The mechanistic attribute of velocity (and associated shear stress) was successful in characterising flow changes during the flood events, and a clear relationship was found between average periphyton development in a large set of streams, and the frequency with which velocities exceeded 1 m $s^{-1}$. Incorporation of this latter measure of disturbance frequency with a second habitat axis describing resource supply (which controls productivity) enabled most of the variance in periphyton development among the study streams to be explained. The actual mechanisms and forces controlling much of the varying resistance and resilience of the periphyton communities were also investigated successfully. Finally, I developed a conceptual model which was useful for predicting biomass and structural characteristics of periphyton communities in two subsequent studies. I hope that this model will be tested in a variety of situations as it shows considerable potential for aiding our synthesis and prediction of patterns of periphyton growth and composition in the stream ecosystems of temperate regions.

**References**

Biggs B.J.F. (1988) Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verhandlungen Internationalen Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1405-1411.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs B.J.F., Duncan M.J., Jowett I.G., Quinn J.M., Hickey C.W., Davies-Colley R.J. & Close M.E. (1990) Ecological characterisation, classification and modelling of

New Zealand rivers: an introduction and synthesis. *New Zealand Journal of Marine and Freshwater Research*, **24**, 277-304.

DeAngelis D.L., Mulholland P.J., Elwood J.W., Palumbo A.V. & Steinman A.D. (1990) Biogeochemical cycling constraints on stream ecosystem recovery. *Environmental Management*, **14**, 685-697.

Douglas B. (1958) The ecology of the attached diatoms and other algae in a stony stream. *Journal of Ecology*, **46**, 295-322.

Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monograph*, **52**, 93-110.

Fisher S.G. & Grimm N.B. (1988) Disturbance as a determinant of structure in a Sonoran Desert stream ecosystem. *Verhandlungen Internationalen Vereinigung fur Theoretische und Angewandte Limnologie*, **23**, 1183-1190.

Grimm N.B. & Fisher S.G. (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, **8**, 292-307.

Mulholland P.J., Steinman A.D., Palumbo A.V. & DeAngelis D.L. (1991) Influence of nutrients and grazing on the response of stream periphyton communities to a scour disturbance. *Journal of the North American Benthological Society*, **10**, 127-142.

Peterson C.G. & Grimm N.B. (1992) Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem. *Journal of the North American Benthological Society*, **11**, 20-36.

Peterson C.G. & Stevenson R.J. (1990) Post-spate development of epilithic algal communities in different current environments. *Canadian Journal of Botany*, **68**, 2092-2102.

Peterson C.G. & Stevenson R.J. (1992) Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*, **73**, 1445-1461.

Peterson C.G., Weibel A.C., Grimm N.B. & Fisher S.G. (1994) Mechanisms of benthic algal recovery following spates: comparison of simulated and natural events. *Oecologia*, **98**, 280-290.

Steinman A.D., Mulholland P.J., Palumbo A.V., Flum T.F., Elwood J.W. & DeAngelis D.L. (1990) Resistance of lotic ecosystems to a light elimination disturbance: a laboratory stream study. *Oikos*, **58**, 80-90.

Stevenson R.J. (1990) Benthic algal community dynamics in a stream during and after a spate. *Journal of the North American Benthological Society*, **9**, 277-288.

Tett P., Gallegos C., Kelly M.G., Hornberger G.M. & Cosby B.J. (1978) Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. *Limnology and Oceanography*, **23**, 785-797.